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Semantic and Conceptual Issues in the Nature-Nurture Problem

The question of what is called "innate" and what is called "acquired" in the behavior of animals, including man, is one that appears regularly and persistently, as a problem and as a source of controversy among students of animal behavior and psychology. This is true in all areas studied by students of behavior. The question of how to formulate the roles of "heredity" and "environment" in the determination of behavior characteristics has agitated students of human intelligence (Anastasi and Foley, 1948), of the abilities for visual perception in higher animals (Hochberg, 1963), of species-typical ("instinctive") behavior in animals (Schneirla, 1956), and virtually every other area of interest to such students.

In the present essay, I propose to discuss the role of the concepts of "innate" and "acquired" in a number of discussions of animal behavior that have occurred in recent years.

Starting in the early 1930's Konrad Lorenz and his students and colleagues developed a conception of the mechanism of "instinctive" behavior which was and is very influential and which has, for a considerable period of time, stimulated a large amount of interesting and creative research. Lorenz's theories (Lorenz, 1937, 1950), developed from work by zoologists on the behavior of lower animals (mostly birds, fish, and insects), formed the basis for a new and flourishing school of animal behavior studies, for which the name "ethology" was adopted.

The term "ethologist" is difficult to define. Insofar as it has a formal definition, it means approximately a scientist who studies the species-typical behavior patterns which constitute part of the animal's biological adaptation to its environment. During the 1940's and 1950's, the term tended to carry the additional informal connotation that a person designated by it was guided in his work primarily by Lorenz's theories of behavior. In recent years, however, it has become clear that the scientists working on the problems, and with the methods, characterized as "ethological," by no means constitute a monolithic body of opinion linked by fidelity to a particular set of theories. The term "ethologist" must therefore refer to a group of people characterized by a common interest in understanding the behavior of animals in relation to their natural environment (including fellow members of the species).

Lorenz's thinking has, from the start, depended very heavily upon the idea that it is always possible and profitable to distinguish "innate" from "acquired" elements of behavior. Lorenz (1965) agrees that "it would be hard to exaggerate the importance attributed by ethologists to the distinction between the innate and the learned." About fifteen years ago, three North American psychologists (Hebb, 1953; Lehrman, 1953; Schneirla, 1956) published discussions which, each in its own way, implied skepticism about both the heuristic value of the traditional distinction between "innate" and "acquired," and the reality of those two concepts as classes into which any given element of behavior could unambiguously be placed. Over the years since then there has been a considerable amount of discussion centering around these critiques (Eibl-Eibesfeldt, 1961; Lorenz, 1961; Thorpe, 1963a, 1963b; Tinbergen, 1963; Schneirla, 1966), culminating in Lorenz's recent (1965) book, *Evolution and Modification of Behavior*.

Since I was the author of one of the papers giving rise to this series of discussions (Lehrman, 1953) and since I have not published any further direct contribution to the discussion during the intervening fifteen years (although I naturally regard my work during that time as an illustration of my point of view), I would like to take advantage of the opportunity offered by this memorial volume, dedicated to the late T. C. Schneirla, to comment on the present status of this discussion, with particular reference to Lorenz's recent (1965) attempt at a definitive resolution. This is especially appropriate, since I regard Schneirla, who was my teacher, as the most creative, the most articulate, and the most consistent modern spokesman for the point of view that the use of dichotomies such as "innate" and "acquired" is restrictive, rather than instructive, in its effects on the analysis of behavior.

SEMANTICS, CONCEPTS, AND FACTS

When opposing groups of intelligent, highly educated, competent scientists continue over many years to disagree, and even to wrangle bitterly, about an issue which they regard as important, it must sooner or later become obvious that the disagreement is not a factual one, and that it

cannot be resolved by calling to the attention of the members of one group (or even of the other!) the existence of new data which will make them see the light. Further, it becomes increasingly obvious that there are no possible crucial experiments that would cause one group of antagonists to abandon their point of view in favor of that of the other group. If this is, as I believe, the case, we ought to consider the roles played in this disagreement by semantic difficulties arising from concealed differences in the way different people use the same words, or in the way the same people use the same words at different times; by differences in the concepts used by different workers (i.e., in the ways in which they divide up facts into categories); and by differences in their conception of what is an important problem and what is a trivial one, or rather what is an interesting problem and what is an uninteresting one.

The Critiques of the Heredity-Environment Dichotomy

INTERACTION OF HEREDITY AND ENVIRONMENT

Hebb (1953) asserted that to make a dichotomy between "innate" and "environmentally-determined" behavior patterns, with the intention of assigning each element of behavior to one or the other of these classes, is misleading because the influences of heredity and of environment are not exerted upon different parts of the behavior (or of the organism), but are effective, in different ways, on the development of the *same* elements. This goes fairly directly to the heart of Lorenz's earlier use of the term "innate," since he has always implied that, if only behavior could be broken up into appropriately defined elements, it should be unequivocally possible to state which ones were wholly innate and which ones were influenced by "learning." In fact, Lorenz's characteristic method of dealing with the role of learning in behavioral development has been to conceive of an interlacement of innate and learned elements, making a chain, or of situations in which a clearly defined aspect of the behavior (e.g., its form) was innate, while another equally clearly defined aspect (e.g., its orientation to the environment) could be described as learned.

This argument of Hebb's is referred to by Lorenz (1965)[1] as the "first behavioristic argument."

ROLE OF ENVIRONMENT IN THE DEVELOPMENT OF SPECIES-TYPICAL BEHAVIOR

Lehrman (1953) and Schneirla (1956) emphasized a somewhat different argument, which was also mentioned by Hebb. They point out that

[1] Except as otherwise indicated, all further references to Lorenz are to Lorenz (1965).

the ontogenetic development of species-specific behavior patterns may often depend upon influences from the environment, which interact with processes internal to the organism at all stages of development, in such a way that it is misleading to label those behavior patterns that seem to depend upon ordinary learning, and those that do not, as "learned" and "innate," with the implication that they have dichotomously different developmental origins. Schneirla (1966), in particular, has used the concept of "experience" to mean all kinds of stimulative effects from the environment, ranging from stimulus-involved biochemical and biological processes (having effects on the developing nervous system) to what we ordinarily call conditioning and learning. He speaks of maturation as "the contributions to development of growth and of tissue differentiation, together with organic and functional trace effects surviving from earlier development." Earlier I had said (Lehrman, 1953):

> The "instinct" is obviously not present in the zygote. Just as obviously it is present in the behavior of the animal after the appropriate age. The problem for the investigator who wishes to make a closer analysis of behavior is: how did this behavior come about? The use of "explanatory" categories such as "innate" and "genetically fixed" obscures the necessity of investigating developmental *processes* in order to gain insight into the actual mechanisms of behavior and their interrelations. The problem of development is the problem of the development of new *structures* and activity *patterns* from the resolution of the interaction of existing ones, within the organism and its internal environment, and between the organism and its outer environment. At any stage of development, the new features emerge from the interactions within the *current* stage and between the *current* stage and the environment. The interaction out of which the organism develops is *not* one, as is so often said, between heredity and environment. It is between *organism* and environment! And the organism is different at each different stage of its development.

The section of my paper in which I made these remarks was called "Heredity-vs.-Environment, or Development?"

It should be obvious from these quotations that what Schneirla and I (and Hebb in a slightly different way) intended was *not* to say that learning was all-important, while accepting the traditional dichotomy that maturation is an unfolding of gene-determined anatomical, physiological, and behavioral patterns (Schneirla, 1966), and that influence from the environment consists solely of conditioning or trial-and-error learning; rather, we were questioning the value of the dichotomy itself, *not* stressing one side or the other of it.

Lorenz calls this type of discussion the "second behavioristic argument."

Some Problems of Definition

My first serious task is to examine some semantic problems: i.e., those arising from the use of words as labels, which may compound the actual problems arising from the conceptions to which the words were intended to apply.

WHO IS AN ETHOLOGIST?

What is the significance of the fact that Lorenz labels the principal considerations introduced by Hebb, Schneirla, and myself as 'behavioristic" arguments? The background for this labeling lies in the repeated assertions made by Lorenz and other writers to the effect that these criticisms arise from the fact that the people who wrote them are psychologists, and are therefore incapable of understanding biological problems. Lorenz refers to "American psychologists" as the source of criticism of his ideas, and repeatedly implies that these critics impute to biologists ideas which they do not hold, the implication being that as psychologists, they are not sensitive to the considerations that are important to biologists.

This type of labeling is, for several reasons, not a very constructive contribution to a discussion of the problems of heredity and development. For one thing, the views of biologists like Hinde (1966) and Tinbergen (1963) are very much like those expressed by these "American psychologists," and the implication that they have been unduly influenced by alien intrusions into their field of work is less than respectful.[2]

For another thing, this kind of labeling tends to arouse (or to reveal) a prejudice against the person being labeled which prevents (intentionally or unintentionally) a full appreciation of his contribution to the discussion. It is too easy to close one's mind to an argument by simply deciding that the source of the argument is an outsider.

Finally, the term "behaviorist" is an affront to the memory of T. C. Schneirla, whose lifelong work was a thoughtful, penetrating and broadly based analysis of the role of physiological, social, and ecological processes, and of the integrations among them, in the development and regulation of the behavior patterns by which the army ants (*Eciton*) are adapted to their environment; of the ways in which different species of these ants differ from each other; of the mechanisms that give rise to these species differences; and of evolution in this group. His work was not remotely related to the tradition of American "rat psychology" to which Lorenz refers by the term "behaviorism." As for me, the reason I chose to study

[2] Hinde (1968), in a paper published while this essay was being set in type, has expressed ideas quite similar to those presented here.

with Schneirla was the same as the reason I chose to become a student of animal behavior: I was interested in understanding the behavior of birds as I had observed it in nature in my youth. If Lorenz intended to be tactful by pointing out that Schneirla and I should not be regarded as biologists, then the intention failed. I would much rather be called stupid!

I should not point out irrational, emotion-laden elements in Lorenz's reaction to criticism without acknowledging that, when I look over my 1953 critique of his theory, I perceive elements of hostility to which its target would have been bound to react. My critique does not now read to me like an analysis of a scientific problem, with an evaluation of the contribution of a particular point of view, but rather like an assault upon a theoretical point of view, the writer of which assault was not interested in pointing out what positive contributions that point of view had made. It does fail to express what, even at that time, I regarded as Lorenz's enormous contribution to the formulation of the problems of evolution and function of behavior, and his accomplishment in creating a school based upon the conception of species-specific behavior as a part of the animal's adaptation to its natural environment. (This would be an appropriate point for me to remark that I do not now disagree with any of the basic ideas expressed in my critique!)

THE MEANINGS OF "INNATE" AND THE MEANINGS OF "INHERITED"

The terms "innate" and "inherited" both have, in different contexts, at least two different meanings, which do not refer to the same processes, which are not arrived at by the same operations, and which have entirely different kinds of reference to the problem of development, but which are often confused with each other.

When a geneticist speaks of a character as inherited, what he means is that he is able to predict the distribution of the character in an offspring population from his knowledge of the distribution of the character in the parent population and of the mating patterns in that population. He is *not* necessarily making any inferences whatever about the developmental processes involved in the ontogeny of the character, or even the extent to which it is subject to change under environmental influence. Another way of saying this is that a character may be said to be "inherited" or "heritable" or "hereditary," if the variation of this character from individual to individual can be shown to arise from differences in the genetic constitution, or genome, of the different individuals, rather than from differences in the kind of environment in which they have been reared, or in the way in which they have been treated. Now, the fact that selective breeding (i.e., arranging for the offspring generations to consist only of individuals resulting from the matings of members of the parent generation which have been selected for the presence or absence of some specific characteristic or characteristics) can result in striking changes in the characteristics of the group of organisms certainly means that the characteristic is hereditary, but it by no means demonstrates that the *same* characteristic cannot be influenced by the environment. A genome arrived at by selective breeding in one environment may have quite different phenotypic characteristics in a second environment, while an environmental change that has great influence upon the phenotypic development of one genome may have no effect upon that of another (Haldane, 1946).

Geneticists have dealt with this problem by restricting the concepts of "heritability" and "environmental influence" with respect to any given character to an estimate of the amount of the actually observed variability in that character that can be attributed to variations among the different genomes *actually tested,* and to the amount that can be attributed to the variety of environments in which organisms with those genomes have *actually been raised.* They thus do not preclude the possibility that other genes than the ones tested might have an effect upon the character, or that environments other than the one tested may cause unpredictable changes in the phenotypic appearance of a given genome. In genetic usage, therefore, the fact that a character can, in a given environment (for example, the "normal" environment) be strikingly affected by selective breeding (as, for example, by hybridization experiments) does not directly deal with the question of whether variations in the environment during the development of the organism would or would not have an effect upon the manner of development of the adult phenotype.

There is, however, a *second* meaning which, implicitly or explicitly, is often attributed to the words "innate" or "hereditary" or "inherited" by students of animal behavior and by nongeneticists generally. This meaning is that of *developmental fixity,* i.e., that the organism is impervious to environmental effects during development, and so it *must* develop characteristics that are preorganized "in the genes," regardless of the environment in which it is reared. Now, I am *not,* at this point (but see below, pp. 28–30), attempting to discuss the question of whether there is such a thing as developmental fixity, or whether the term "innate," meaning unavailable to environmental influence, is a useful or meaningful term to apply to behavior characteristics. I am merely trying to point out that the concept of "innateness" as referring to developmental fixity is a *different* concept, and one that exists in a different, and not parallel, dimension, from the concept of "alterable by selective breeding," which is the same as "achievable by natural selection."

But it must be obvious to every candid observer of the literature of animal behavior that these two different, and incommensurate, concepts are very often implicitly mixed into one use of the term "innate." This is, for example, what Lorenz does when, in a discussion about the legitimacy of the use of the term "innate," he introduces as evidence both the fact that the offspring of a hybrid shares behavioral characteristics of both parent species and the fact that learning does not influence the development of the behavior patterns concerned.

LORENZ'S USE OF "INNATE"

Lorenz did not identify the distinction outlined in the preceding section, or the problems raised by it, because his recent discussion was couched in somewhat different terms. He has, however, proposed a very interesting resolution of the problem as he perceives it. He states that the term "innate" should "never, on principle, be applied to organs or behavior patterns, even if their modifiability should be negligible." He does, however, think it proper to describe as "innate" a distinctive *property* of a neural structure, such as its ability to select, from the range of available possible stimuli, the one which specifically elicits its activity, and thus the response seen by the observer. Presumably, the property of the neural structure in giving rise to a particular movement pattern would also be a property of this kind, which Lorenz refers to as a "character." He is thus making a distinction between organs, structures, and behavior patterns, which he says should not be called "innate," and special properties of these organs, structures, and behavior patterns, by which they fit into the appropriate environment. His conception is that, even if, for example, an animal can see nothing without previous visual experience at the appropriate time in its development, it might still be that if it had appropriate experience (i.e., experience of light, or of contours, etc.), some of its specific responses could be linked to specific visual stimulus configurations, *without* the animal having had any *specific* visual experience that would account for its reaction to those visual stimuli, rather than to others. In this context, he asserts that the "information" that the following response of a given species of fish is elicited by the characteristic color of the mother fish of that species, rather than by other colors, may legitimately be called "innate," if it can be demonstrated that a fish that can see will prefer to follow this color, without any previous experience of the color, even though it may be true that the development of visual abilities in the first place required experience of light. In this situation, he would not call the visual capacity as such innate, but only a specific property of the fish's visual system: that it was capable of selectively responding to the appropriate color when the animal was in a mood to follow.

This distinction is made in the service of a more fundamental distinction, which is the principal argument of Lorenz's book and the principal basis for his insistence that the concept of "innateness" is an objective and necessary one. Briefly, Lorenz states that, when a behavior pattern is adapted to a given aspect of its environment, the "information" which defines the properties by which the behavior pattern is adapted to the environment can have been incorporated into the behavior pattern of the animal either by "the adaptive processes of evolution" or by "individual acquisition of information." By "adaptive processes of evolution," Lorenz refers to the creation of the genome by natural selection, so that the gene-complex characteristic of an individual is the result of a history of selection for those genes that, in the natural environment, give rise to characteristics that are adaptive to that environment, including behavior characteristics. This is a sort of historical "trial and error" process, in which mutations that lead to useful (i.e., adaptive) results are retained, while those that lead to harmful (i.e., nonadaptive) ones are eliminated. By "individual acquisition of information," Lorenz means individual learning.

Lorenz's present argument is that behavior characteristics that are adaptive to particular points of the environment must be considered "innate" if their source, or provenance, is through the incorporation of genes into the genome through natural selection, and must be considered "learned" if their source is a change in the behavior of the animal as a result of its individual experience of that environment.

Up to this point, my purpose has been to outline the type of behavior about which opposing views have been expressed, to sketch, however briefly, the nature of the disagreements, and to point to some problems involved in defining the terms about which the disagreements have flowered. I should now like to turn to a consideration of some conceptual problems, with a view to pointing out some ways in which different workers disagree in their evaluation of the importance of various questions, even when they agree about the facts concerned.

VARIATION AND DEVELOPMENT

Genetic Variation Versus Developmental Process

If we rear two animals in the same environment, and they develop different behavior patterns, it is perfectly clear that the difference in the behavior patterns depends upon differences in the genetic constitution of the animals, and not upon differences in the environment. One might refer to these *differences* as "innate," meaning only that they depended upon differences in the genome. This use of the term "innate" would be meaningful and useful, provided it was recognized that the observations that justified the conclusion that the difference between the two animals was a genetic difference do not necessarily imply anything, one way *or* the other, about the extent to which the development of the character concerned is, in either animal, influencible by changes in the environment.

This is the situation in which we find ourselves when we compare different species living in similar environments, and showing different behavior. The differences between the species obviously arise from genetic differences, and it is perfectly appropriate to use genetic terms, and terms deriving from considerations of evolutionary adaptation, in analyzing these differences and their evolutionary relationships, and the evolutionary origins of particular behavior patterns. None of these considerations, however, really bears on the question of ontogenetic origin, which is, to some degree, a question of a different kind.

To take a rather simple example, let us consider one aspect of the problem of the role of behavior patterns in the formation of species. An existing species becomes divided into two descendant species when two parts of the original population become geographically separated from each other and when, under conditions of geographical separation (i.e., when no genes are being exchanged between one population and the other), they become so different from each other genetically that they would not interbreed if the geographical barrier were removed. This may happen because, while they were in geographical isolation, they evolved in slightly different directions as a result of adaptation to slightly different environments, or it might occur because the populations were small enough so that rarely occurring mutations occurred, by chance, in different frequencies in the two populations, or it might come from some combination of these and similar factors. Whatever the reason, each of the two populations may eventually consist, more or less homogeneously, of individuals that will be sufficiently different from those of the other population so that they will no longer be as ready to mate with them as they would be with members of their own population. This may be because the members of the two populations prefer different habitats and thus do not meet each other, because the courtship behavior of a member of one population is no longer adequately stimulating to a member of the other, or for a variety of other reasons, behavioral, ecological, or morphological. Now, this "reproductive isolation" may not be complete at the time the geographical barrier between the two populations is removed. It may be that, at the time it becomes geographically possible for the two populations once more to become continuous, there has developed only a relative isolation, defined as a quantitative preference for mating with a member of the animal's own population, rather than a member of the other. In that case, a number of things may happen, the extremes of which might be defined by two alternative outcomes: (a) if the two populations are similar enough to each other so that hybrids between them can survive in the existing range of environments as well as can members of either population, the two populations may simply merge, as the genes of one are spread

through the other through the hybrid matings at the points where the populations meet each other; and (b) the two populations may have become so different from each other, and adapted to such different environments, that hybrids between them will not be as well adapted for survival in *any* environment as each of the populations is to *some* environment. These hybrids will be at a selective disadvantage, compared with the offspring of within-population members of either population. In this case, the hybrids will be eliminated by natural selection, which means that, at least in the zone of overlap between the two populations, only those genomes will survive that ensure, in that environment, a preference against mating with a member of the other population (Mayr, 1942).

This process can be reproduced experimentally in the laboratory. For example, Koopman (1950) allowed individuals of two species of *Drosophila* to select mates in a mixed population. There was a moderate degree of preference for mating within the species, as could be seen by the characteristics of the larvae (the animals carried a marker gene, which made it possible to distinguish a hybrid animal from pure-bred animals in the larval stage). He removed all the hybrid larvae, and then allowed the remaining members of the offspring generation to choose mates again from a mixed population, now consisting only of the offspring of animals that had selected members of their own species for breeding. He repeated the process for a number of generations, thus tending to eliminate those genes that made possible the selection of a mate from the "wrong" species. The result was that the degree of reproductive isolation (i.e., the strength of the tendency to select a mate from within one's own species) was gradually increased.

In all these examples, the characteristics that insure that the animals will mate only with members of their own population have been arrived at entirely by selection directed against those genes that made possible a maladaptive mating choice. That is, they have been arrived at by the adaptive processes of evolution. This process is very common in nature, and may probably be assumed to have taken place in almost every case where two closely related species breed in the same area. If, however, an animal is reared in association with members of another, closely related, species, it soon becomes clear that in some cases, such as the cowbird, the rearing conditions have no effect upon the mating preferences, while in other cases, such as some species of doves (Whitman, 1919), the mating preferences may be strongly affected, being shifted sharply in the direction of a willingness to mate with a member of the "foster" species (Mayr and Dobzhansky, 1945)! In both cases, the features of the animal that are, in normal circumstances, responsible for its absolute preference for mating with a member of its own species, have been incorporated by natural selection, by selective breeding, by "the adaptive processes of evolution." But in one case, these features include a role of learning, in the other case not! Nature selects for *outcomes:* it does not care whether this outcome is arrived at through the development of features of the animal that make it impossible for it to respond to stimuli offered by members of the other species, or whether it is arrived at through the development of features that make the animal prefer to mate with a member of the species that it experienced in its early life!

Now, I would not dream of implying that Lorenz, the discoverer of imprinting, does not know all that I have just said, and I am aware that his way of dealing with these facts would be to call the preference of the cowbird innate and that of the dove learned. I am merely pointing out that if a scientist is not overwhelmingly convinced that characteristics incorporated into the species by the actions of natural selection are, *by that fact,* demonstrated to be impervious to individual experience, he is not necessarily guilty of "a very deep misunderstanding of biological ways of thinking" or "a lack of acquaintance with phylogenetic and genetic thought" (Lorenz, 1965).

What I intend to indicate by the example that I have just given is that the clearest possible genetic evidence that a characteristic of an animal is genetically determined in the sense that it has been arrived at through the operation of natural selection does not settle any questions at all about the developmental processes by which the phenotypic characteristic is achieved during ontogeny.

Genetics and Developmental Fixity

In the crustacean *Gammarus,* the difference between the normal red eye-color and a mutant with chocolate eyes depends upon a single mutation which affects the rate at which an eye pigment is deposited during a certain stage of development. If the mutant is reared below a given threshold temperature, the eyes will develop red, and at intermediate temperatures there will be intermediate eye colors (Ford and Huxley, 1927).

Variations in the wing structure of *Drosophila melanogaster* may be affected by a wide variety of genetic mutations (Morgan, Sturtevant, Muller, and Bridges, 1923). These mutations also have an effect upon the ability of the animal to fly. Different flies of a single genotype may be able to fly normally, weakly, or not at all, depending upon the temperature at which they are raised (Harnly, 1941).

These two examples (which, let me hasten to add, will not surprise any biologist) show that the same genes may lead to different phenotypic outcomes when the animal is subjected to different environmental influences during development. Suppose, however, that *Gammarus* or *Drosophila* were, for reasons having nothing to do with the mechanisms of eye development or wing development, unable to survive at any temperature outside the range 24°–26° C. In that case, we would have to say that the character was uninfluenced by the environmental temperature. But would this mean that the mechanism of eye development, or of wing development, was any different? I think not. Further, the situation would be similar if, instead of being unable to survive temperature variations, the animals possessed regulative mechanisms that maintained the temperature environment of the eye (or of the wing) constant in spite of variations in environmental temperature. In both of these cases the outcome of the experiments would be that we had failed to show any effect of environmental temperature upon the development of eye color, or of flying ability. But this would not *necessarily* mean that considerations of temperature were irrelevant to the development of these characters. Further, it should be clear that the failure to show the effects of a particular environmental variable does not say anything positive about the processes involved in the development of any character.

There is a fundamental question of logic involved here. I am sure that Lorenz and his colleagues perceive those of us who are oriented by Schneirla's teaching as constantly engaged in an eager search for any little snippets of evidence that learning has any effect, however small, on the development of a behavior pattern, to the exclusion of any attention to the broad problems of adaptation, and that we exaggerate the relative importance of learning influences in the service of a need to see learning everywhere and heredity nowhere. Given the role played by the phenomena of adaptation, and by the concept of the "normal environment" in Lorenz's thinking, I can certainly understand how this impression could arise. But that is not at all our conception of our situation. It seems to us that an experimental manipulation that causes a change in the behavioral outcome has thrown some light on the process by which the behavior develops, while an experimental manipulation that *fails* to cause any change in the outcome has *failed* to throw light upon the nature of the processes leading to the outcome. To Lorenz, the failure of an experimental treatment to cause any change in outcome seems just as illuminating as does the success of an experimental treatment in affecting the outcome. He makes this quite explicit when he says that he disagrees with the formulation that "it is not characters but differences between characters which may be described as innate," and says that "the opposite formulation is at least as workable: calling innate the similarities of characters developing under dissimilar rearing conditions." To an *experimental* scientist, the insight gained by observing that a variety of treatments all failed to have any effect is not at all equivalent to that gained by observing that some treatments have effects, while others do not. Indeed, it is of the essence of the experimental method that an experiment cannot be regarded as making a contribution to the understanding of any problem unless the experimenter has succeeded in finding alternate treatments that have different effects upon the outcome. It is for this reason, and not because I think that any *particular* kind of developmental influence is all-important, that I regard an experiment that shows an effect, during development, of any treatment, as a contribution to the illumination of a process of development, while a study which succeeds only in showing that some types of manipulation have no effect upon the outcome seems only like a challenge to follow the problem to an earlier stage of development, or to a more intricate level of physiological analysis.

The criterion of developmental fixity is thus a negative one in the sense that it is based upon the *lack* of effect of experimental treatments. If a class of behavior patterns is defined in large part by such a criterion (lack of effect of treatment), as in Lorenz's classification of the instinctive act (*Erbkoordination*), the assumption that all members of the class have *developmental* or *physiological* features in common is not necessarily valid.

LEARNING, EXPERIENCE, AND DEVELOPMENT

Learning and Experience

One persistent difficulty is that Lorenz, and a number of other writers, use the term "learning" to refer solely to the kind of conditioning and associative learning that are traditionally described as the learning capacities of adult animals (Kimble, 1967), and they have made no effort to incorporate into their thinking Schneirla's concept of "experience," which refers to a wide range of processes, of which learning is only a relatively small part.

Let me repeat Schneirla's definition of "experience": the contribution to development of the effects of stimulation from all available sources (external and internal), including their functional trace effects surviving from earlier development (Schneirla 1957, 1966). Contrast this with Lorenz's statement: "Not being experimental embryologists but students of behavior, we begin our query, not at the beginning of the growth, but at the beginning of the function of such innate mechanisms." By this statement, Lorenz is asserting that he is simply not interested in the type of question to which Schneirla's conception addresses itself. Now, it is not at all necessary that the problem of development should be a central problem for every scientist interested in behavior, or that all students of behavior who are interested in problems of development should be interested in the development of the same types of behavior, or should be primarily concerned with the same stages of development. I think it is important, however, to recognize that there are differences of attitude involved in these disagreements, which do not have to do with factual matters, but with what each of the parties considers to be an interesting problem, or a heuristically significant question. As Lorenz states, he is really not interested in the origins of behavior patterns at those stages of development before they begin to exist as modes of adaptation to the environment. Since his interest starts at that point, it is quite understandable that the only kind of experience that would seem theoretically relevant for him would be the kind of conditioning and associative learning characteristic of animals whose behavioral organization is already ontogenetically well formed. In effect, Lorenz would like to consider the problems of experience solely in terms of the role of conditioning and associative learning in the behavior of animals, starting at stages of development when their species-specific behavior patterns are already functional, so that the problem becomes merely one of whether an animal can learn to use a nesting material other than the ones for which its normal movements are adapted, or whether it needs to have seen a red object in order to prefer to attract a fellow-member of the species with the red belly, or whether it will respond appropriately to the sound of a young animal of its species without ever having heard one before, etc. Problems of the sort referred to by Schneirla would then be left to "experimental embryologists."

This feeling on Lorenz's part is consistent with his assertion that the innate is what must be there before learning begins. However, there is already evidence that the development of organisms is not divided into such convenient chapters, corresponding to the divisions among the professional specialties of biologists. Conditioning can occur very early in life, even prenatally in mammals (Spelt, 1948; Prechtl, 1965), or pre-hatching in birds (Gos, 1935; Hunt, 1949; Sedláček, 1962, 1964; Gottlieb, 1968). For a scientist who is *primarily* interested in the analysis of development, the existence of such early conditioning abilities cannot seem irrelevant to the problem of the ontogenetic origin of later-appearing behavior patterns.

Further, nonbehavioral physiological regulations and those that are of interest to a student of animal behavior cannot be sharply separated. Physiological events that are not normally or conventionally regarded as a part of "behavior," such as changes in body temperature, changes in bladder activity, changes in kidney activity, changes in tension in the mammary gland, dilation and constriction of the blood vessels, are all to some degree under neural control, and can be conditioned, both by Pavlovian techniques (Bykov, 1957) and by those of operant conditioning (Miller, 1969; Miller and di Cara, 1967). In addition, the conditioned stimuli may be either external stimuli or stimuli arising inside the body, including stimuli arising from changes in tension elsewhere in the body, which may themselves be conditioned (Razran, 1961). This means that the distinction between "animal behavior" and other kinds of physiological regulation are not as absolute in the organization of the animal's physiological mechanisms as they usually are in the perception of the student of animal behavior, and that it may be necessary for scientists interested primarily in animal behavior to pay attention to a great many things that are primarily of interest to other kinds of scientists (such as experimental embryologists, or even psychologists) in order to achieve a broadly based understanding of the origins and organization of the phenomena that attract their primary interest.

The separation of problems into those visible after the adaptive behavior patterns begin to function, and those which are relevant to early development (the former being the province of the student of animal behavior, while the latter is assumed to be of interest only to experimental embryologists), presupposes that it is possible to make a sharp distinction between learning and other contributions of experience to development, and that there are no intermediates. As Schneirla has repeatedly pointed out, however, sharp lines cannot be drawn, in early stages of development, between: the effects on neural development of nonbiological conditions (temperature, light, chemical conditions in the environment); nonspecific effects of gross stimulus input; the developmental effects of practice passively forced during ontogeny; the developmental effects of practice resulting from spontaneous activity of the nervous system; links and integrations between behavioral elements, resulting from early, nonfunctional partial performances; interoceptive conditioning resulting from inevitable tissue changes and metabolic activities; simple conditioning to stimulation resulting from spontaneous movements; and simple instances of conventional conditioning and learning.

Now, the introduction of the concept of "experience," in the sense described here, into the discussion of development is by no means equivalent to saying that all behavior patterns derive from learning. This point has been repeatedly made by Schneirla over many years, and I was quite aware of it when I wrote my first contribution to this discussion fifteen years ago. To quote a characteristic remark from that paper (Lehrman, 1953):

> . . . Analysis of the developmental process involved shows that the behavior patterns concerned are not unitary, autonomously developing things, but rather that they emerge ontogenetically in complex ways from the previously developed organization of the organism in a given setting. . . . The post-hatching improvement in pecking ability of chicks is very probably due in part to an increase in strength of leg muscles and to an increase in balance and stability of the standing chick, which results partly from this strengthening of the legs and partly from the development of equilibrium responses . . . Now, isolation or prevention-of-practice experiments would lead to the conclusion that this part of the improvement was due to "maturation." Of course it is partly due to growth processes, *but what is growing is not pecking ability or anything isomorphic with it.* The use of the categories "maturation-vs.-learning" as explanatory aids usually gives a false impression of unity and directedness in the growth of the behavior pattern, when actually the behavior pattern is not primarily unitary, nor does development proceed in a straight line toward the completion of the pattern.

As I reread that paper, it seems clear to me that, even at that early stage, I was not insisting that all behavior is learned, but that the distinction between "innate" and "acquired" is an inadequate set of concepts for analyzing development, and that the development of behavior patterns could not be analyzed by assuming autonomously developing specific substrates for each behavior pattern, isomorphic with the behavior.

These remarks are my reaction to a recent rereading of my 1953 paper. In the intervening years, I have heard it so often said that I believed that all species-specific behavior develops through individual learning that I almost came to believe that I *had* said it! I remember reading a discussion in which I. Eibl-Eibesfeldt and W. H. Thorpe apparently succeeded in convincing an initially incredulous Donald Hebb that I had insisted that all behavior is learned through individual experience (Eibl-Eibesfeldt, 1961)!

I believe this difficulty arose from the fact that many workers in the field of animal behavior had such a firmly fixed opinion that every element of behavior ought, on *logical* grounds, to be clearly classifiable as "innate" or as "learned," that any discussion that cast doubt upon the usefulness of the concept of "innate" must inevitably have seemed like an insistence that all behavior must belong to the other category! As I know from my own experience, this could be so even when the discussion in question was addressed, not to the thesis that all behavior is learned, but to the thesis that the dichotomy *itself* does not adequately express the necessities for developmental analysis of behavior.

Is Development Necessary?

THE IDEA OF A "GENETIC BLUEPRINT"

The idea of a genome as a "blueprint," contained in the fertilized egg and representing a plan for the construction of an adult organism, is a very attractive one. Lorenz says that "what rules ontogeny . . . is obviously the hereditary blueprint contained in the genome and not the environmental circumstances indispensable to its realization. It is not the bricks and the mortar which rule the building of a cathedral but a plan which has been conceived by an architect. . . ." Further, he says that ". . . our first question concerning the ontogeny of an organism and its behavior is: 'What is blueprinted in its genome?' "

Now, it may be comforting, in the sense that it gives us the feeling that we have increased our understanding of the problem, to say that a behavior pattern (or a structure) is innate if it is "blueprinted in the genome" or, in a more modern vernacular, "encoded in the DNA." There are, of course, contexts in which such expressions are meaningful, but I believe that the comfort and satisfaction gained from disposing of the problems of ontogenetic development by the use of such concepts are misleading, and are based upon the evasion or dismissal of the most difficult and interesting problems of development.

It seems to me that there is a fundamental fallacy in the use of the analogy of the relationship between a blueprint and the structure represented by it to represent the relationship between the genome at the zygote stage and the phenotypic adult. A blueprint is isomorphic with the structure that it represents. The ratios of lengths and widths in the blueprint are the same as those in the structure; the topographical relationships among the parts of the structure are the same as those among the corresponding parts of the blueprint; each part of the structure is represented by a separate part of the blueprint, and each part of the blueprint refers only to a specific part or parts of the structure. It will be immediately obvious that this is profoundly different from the relationship between the genome and the phenotype of a higher animal. It is *not* true that each structure and character in the phenotype is "represented" in a single gene or well defined group of genes; it is *not* the case that each gene refers solely, or even primarily, to a single structure or character; and it is *not* the case that the topographical or topological relationships among the genes are isomorphic with the structural or topographical relationships among phenotypic structures to which the genes refer. It is, of course, a commonplace of modern biology to say that each gene is responsible for the production of a single enzyme. This formulation reflects the truly enormous advances that have been made in recent years in understanding the structure of the genes, primarily on the basis of research on the biochemical actions of genes in one-celled organisms. The problems of ontogeny and differentiation of structures in complex organisms, however, have hardly been touched as yet by the recent massive advances in molecular biology. A facile description of the genome as a "blueprint" gives a misleading impression of understanding a problem that is regarded by modern geneticists as one of the major unsolved problems of biology, and which ought to be regarded as a truly difficult problem by *any* biologist, even a student of animal behavior who is prepared to leave the problem to the experimental embryologist.

Another problem with the conception of the genome as a "blueprint" is, of course, that, while it poses as a contribution to the understanding of ontogeny, it is actually *irrelevant* to the question of individual development. As Lorenz himself says, ". . . it is perfectly possible that a particular motor sequence may owe to phylogenetic processes all the information on environment underlying its adaptiveness and yet be almost wholly dependent upon individual learning for the 'decoding' of this information." But it should be perfectly clear that, if a character "encoded" in the genes may or may not require individual experience for its development, then a scientist who is interested in the causal analysis of development is not helped very much by statements about the "encoding" or "blueprinting" of complex characters in higher animals. Here again, I repeat that the concept of "innate" in the sense of determination by the genome, and the concept of "innate" in the sense of imperviousness to individual experience, refer to different problems and relationships, which cut across each other, rather than making a single conceptual whole. And here again Lorenz, by inconspicuously merging these two conceptions into a single usage, is led to speak of patterns as being blueprinted in the genome, *as opposed to* being based upon experience, while simultaneously acknowledging that patterns "blueprinted" in the genome may or may not develop through individual experience.

It seems to me, then, that although the idea that behavior patterns are "blueprinted" or "encoded" in the genome is a perfectly appropriate and instructive way of talking about certain problems of genetics and of evolution, it does not in any way deal with the kind of questions about behavioral *development* to which it is so often applied.

PROVENANCE AND ONTOGENY

In my 1953 critique, I referred to the work of Kuo (1932a, b, c, d), who made detailed observations of the behavioral development of the domestic chick embryo within the egg. On the basis of these observations, Kuo suggested that the pecking behavior that can be seen in chicks immediately after hatching develops through a series of stages in which the neck is first (early in embryonic life) passively bent when the heartbeat causes the head (which rests on the thorax) to rise and fall, with active bending of the head occurring later, at first in response to tactual stimulation. Kuo also suggested that the opening and closing of the bill (associated with pecking in the post-hatching animal) first occur when the bird's head is nodding during the embryonic period, apparently through nervous excitation furnished by the head movements through irradiation in the still-incomplete nervous system, while the opening and closing of the bill become independent of head activity only somewhat later. Kuo noted that fluid forced into the throat by movements of the bill and head apparently causes swallowing, beginning at a characteristic time during embryonic development. Kuo's suggestion was that the movements forced by the timing and order of development of the various structures, neural and motor, and by the conformation of the bird's body enforced by its position within the egg, provided an experiential contribution to the development of the integration of the head, bill, and throat components of the food-pecking lunge, which is already to be seen (although in incompletely integrated form) by the time of hatching. It has recently become clear that some aspects of the development of motility in the chick embryo do not depend upon sensory input (Hamburger, 1963; Hamburger, Wenger, and Oppenheim, 1966), and caution is required in interpreting Kuo's data, which have not yet been subjected to direct experimental test. However, the existence of conditioned responses several days before hatching is very well established in these birds (Gottlieb, 1968; Sedláček, 1962, 1964), and the nature of behavioral and neural development during embryonic life in birds, and the problem of the role of experience at this stage, are being actively investigated in several different laboratories (see Gottlieb, 1968, for review).

Of this discussion, Lorenz says "If Lehrman (1953) gives serious consideration to the assumption that a chick could learn, within the egg, considerable portions of the pecking behavior by having its head moved rhythmically up and down through the beating of its own heart, he totally fails to explain why the motor pattern thus individually acquired should fit the requirement of eating in an environmental situation which demands adaptedness to innumerable single givens. . . ."[3]

Here I must repeat something I said earlier in this essay. Nature selects for *outcomes*. Natural selection acts to select genomes that, in a normal environment, will guide development into organisms with the relevant adaptive characteristics. But the path of development from the zygote stage to the phenotypic adult is devious, and includes many developmental processes, including, in some cases, various aspects of experience. This is clear from many considerations, and is acknowledged by Lorenz himself. What then is the difficulty about assuming that, *whatever* the characteristics

[3] This is Lorenz's oversimplified version of my own description, which was a very cautious description of what I imagined to be a very complex series of events, in connection with which I did not use the word "learning." I did refer, at one point in a 500-word description of Kuo's observations, to a "process of development, which involved conditioning at a very early age. . . ." Even fifteen years ago, under Schneirla's influence, I was trying to convey the idea of continuity and interpenetration between the processes of growth and those of the influence of environment, and to express a feeling of tentativeness and ambiguity about the distinction between the effects of experience on a developing organism and the effects of experience in a mature nervous system. And even today Lorenz is perfectly confident of the sharpest distinction between "morphological ontogeny producing structure" and "trial-and-error behavior" producing learning, with no sense of difficult intermediates or unsolved conceptual problems.

of the developing nervous system, they must be such as to give rise to the adaptive form of pecking which is seen after the bird hatches? The relationships described by Kuo, involving certain putative effects of experience that might be inevitable in the context of the developing structures in the egg, are no more mysterious a product of embryonic development than any other characteristics of the developing nervous system. It does not matter to the process of natural selection whether what is being selected for is a genome that gives rise to adaptive pecking at food through a developmental process that does not involve experience, or whether it is a genome that gives rise to adaptive pecking behavior via a course of development that *does* include effects of experience. This is another case in which the statement that a characteristic has been arrived at through selective breeding (i.e., in this case, through natural selection) says nothing at all about whether its development does or does not include an effect of experience. Natural selection can select for specific ways of being sensitive to experience, or for phenotypic structures that make experience possible, just as readily as it can for any other characteristics.[4]

In the same context, Lorenz speaks of "some American psychologists" as "trying to avoid, at all costs, the concepts of survival value and phylogenetic adaptation for no other reason than that they regarded them as 'finalistic.'" As I hope the discussion so far has made clear, however, I have not been trying to avoid the concepts of survival value and phylogenetic adaptation, but only to prevent them from being merged with the concepts of the *causal* analysis of *development*, in order that the understanding of ontogeny should not be confused by merging two different meanings of the term "innate," which are to some extent irrelevant to each other.

Lorenz's objection to the formulation that "it is not characters but differences between characters which may be described as innate" is not as clear as he implies. The concept of evolutionary adaptation is not arrived at, and is not maintained in the minds of observers, by perceiving one animal or one species in its adaptation to the environment. The concept of adaptation, both historically and in its everyday application, depends upon the fact that we observe *different* species to show elaborate adaptations to *different* environmental requirements. The adaptive elegance of the way in which a newly hatched pheasant pecks at food on the ground is fully apparent only to the observer who is on some level aware, while he

[4] Hamburger's recent work (1970), makes it clear that Kuo's conceptions of the sources of early behavioral organization in the chick embryo are not tenable, and are based on incorrect assumptions about the embryology of the chick's nervous system. Lorenz's feeling and mine was wrong. I would not now use Kuo's work as an example of the study of behavioral development. I have, however, retained the present discussion of Lorenz's reaction to it because it still illustrates the conceptual and methodological problem I am discussing here.

watches the pheasant, that a newly hatched thrush would not peck at the ground, but would gape (beg) from its parent, who would be willing to feed it in a way of which the parent pheasant is incapable. Lorenz makes this quite explicit when he says (of Kuo): "It also remains unexplained why only certain birds peck after hatching, while others gape like passerines, dabble like ducks, or shove their bills into the corner of the mouth. . . ." Here Lorenz clearly, if inadvertently, acknowledges that it is the *differences* among the behavior patterns of different species living in similar environments that give rise to the sharp feeling, which I share, that the species have different genomes. It remains true, of course, that differences in the genome may give rise to differences between animals, at a very early stage of development, which *consist* of differences in the extent to which they are able to take advantage of information offered by the environment, or differences in what they will pay attention to in the environment. Therefore, although animals reared in the same environment that behave differently must have started with different genomes, this does not in any way tell us whether or to what extent differences in experience might have played a role in the development of the phenotypic differences between them as adults.

NORMAL AND ABNORMAL

The differences in attitude and interests between scientists whose primary interest is in evolution and adaptation and those whose primary interest is in the causal analysis of development are fairly well demonstrated by Lorenz's reaction to a paper by Donald Jensen (1961). Jensen had suggested that many operations other than genetic selection or training could produce differences in behavior between animals. These operations include nutritional variations, alterations of the nervous system, hormone treatments, etc. Jensen suggested that studying the effects of a wide range of differential treatments upon the development of behavior differences, with the intention of inductively integrating the information thus acquired, would be a more fruitful and less controversial way of coping with problems of ontogeny and of causality than the prevalent attitude of treating the question "innate or learned?" as a primary and ultimate question on which all others must hinge.

This modest suggestion has aroused a special ire in Lorenz, which is noticeable even against the background of the generally indignant tone of his book. This is because, in Lorenz's opinion, the investigation of the effects of a very wide variety of treatments which can alter the behavior runs directly counter to the main task of the biologist: to understand how the genome that is arrived at by natural selection gives rise, in the *normal*

environment, to the *normal* behavior pattern adapted for that environment.

Lorenz's concern that the introduction of "abnormalities" will distort and misrepresent the study of adaptive characters is shown by the following selection from his remarks:[5]

> Non-adaptive differences in structure and behavior are of but secondary interest to the biologist, while they are the primary concern of the pathologist. . . . As students of behavior, we are not interested in ascertaining at random the innumerable factors that might lead to minute, just bearable differences of behavior bordering on the pathological. What we want to elucidate are the amazing facts of adaptedness. . . . We need not bother about the innumerable factors which may cause "differences" in behavior as long as we are quite sure that they cannot possibly relay to the organism that particular information which we want to investigate.

Now, Lorenz is quite right to point out that experimental treatments cannot be selected at random; they must be chosen with some intuitive feeling for their relevance to the normal phenomenon, the development of which we wish to understand. I am not persuaded, however, that the distinction between "pathological" and "normal" is a very useful guide for understanding the causes of development; and I am not convinced that a biologist interested in understanding *development* is obligated to recoil from any treatment that disturbs the "very complicated and very finely balanced system" (Lorenz, 1965) which is the living organism. Indeed, a very good case can be made for the proposition that it is precisely by interfering with normal development and noting in what way the resulting abnormalities develop that we gain the most illuminating insights into the normal processes of development.

Experience and "Normality"

Lorenz's tendency to regard conventional learning paradigms as the only method for defining environmental influences that are of any interest to a student of behavior expresses itself in a tendency to regard any other developmental effect of experience as simply a pathological effect of "bad rearing." This distinction is very clear, for example, in his statement that "we try to produce an individual whose genetical blueprints have been realized unscathed in the course of healthy phenogeny. Should we fail in this, we would incur the danger of mistaking some effects in our subject's behavior for the consequences of information withheld, while they really are the pathological results of stunted growth."

[5] These sentences are not consecutive in Lorenz's text but occur, with intervening text, in the space of a page or so.

This is, of course, a logical extension of Lorenz's position that, with the exception of trial-and-error learning or classical conditioning in the fully developed nervous system, the effects of stimulation from the environment during development are matters of interest, not to the student of animal behavior, but to the experimental embryologist or the pathologist.

I think, however, that it is not so easy as Lorenz implies to make sharp distinctions between "learning" and "mere" pathologies of development. Let us look at some examples of the effects of rearing in abnormal conditions upon behavioral adaptations:

1. In many species of birds, the young characteristically follow their parents about within a very short time after emerging from the egg. It has been clear since the early work of Lorenz (1935) that, in many ducks, geese, and other species of precocial birds, the ability of the young to follow selectively adults of their own species is dependent upon a very quick learning process which occurs during a restricted period very early in life; the birds thus learn through this "imprinting" experience to follow the models that they experience immediately after emerging from the egg. These will, in nature, usually be the birds' parents. If newly hatched ducklings are exposed to adult ducks of another species than their own, they may later prefer to mate with the members of the species on which they were imprinted, rather than with members of their own species (Schutz, 1965). This may happen either through long-term effects of the early experience, or through intervening (adolescent) experience with birds with which they associate because of the earlier experience (Hinde, 1962; Bateson, 1966). Now, a bird which, because of this early experience, wants to mate only with a member of another species, which refuses to mate with it, has certainly had its development altered in an abnormal direction; it is pathological, since the abnormal conditions of its development have led to an adult condition in which it is no longer adapted to its environment. This treatment, which is widely and correctly regarded as demonstrating, for the student of development, a form of learning, must also be regarded, for the student of evolutionary adaptation, as an example of pathological interference with an evolutionary adaptation through rearing in an abnormal environment.

2. When Harlow reared rhesus monkeys without giving them any opportunity to interact with age-mates, they developed striking and pervasive abnormalities of behavior: as adults, they were not able to maintain social contact with other monkeys, their sexual behavior was so drastically interfered with that most of them were totally unable to copulate, and the balance between the role of fear and aggression and the role of more positive social responses in the social relationships of these monkeys was

severely distorted. The deprived monkeys, in general, were incapable of normal integration into a group of monkeys. This distortion of the normal early experience apparently has widespread effects upon the emotional responsiveness of these monkeys, which are reflected both in specific distortions of particular behavior patterns and in more general interferences with a wide range of behavior patterns (Harlow and Harlow, 1965).

3. The rat shows a characteristic response of fear and anxiety to a strange environment. The level of this response and many details of it can be altered by selective breeding, and are therefore heritable in the geneticist's use of the term (Fuller and Thompson, 1960). The rat also shows a characteristic tendency to be curious about a novel environment, and to explore it (Berlyne, 1960). The tendency to explore a novel environment (and thus to find food and a nesting place) and the tendency to be fearful of it (and thus to avoid precipitate entry into new areas where predators might be lurking) are both adaptive, and the balance between these two tendencies is undoubtedly arrived at through natural selection. This balance is *also* arrived at through early experience, however, and the amount of fearfulness shown by adult rats introduced into a strange environment can be substantially influenced by early weaning, by handling during early life, or by preweaning experience with different types of mother (Beach and Jaynes, 1954; Levine, 1962; Denenberg and Whimbey, 1963). The "normal" amount of fearfulness shown by a rat in a strange environment is therefore in part a function of the way in which its mother treated it during its infancy. It is impossible to say that the rat has "learned" anything about the characteristics of the environment (including the predators) to which it will later respond; it is equally impossible to deny that the response to the strange environment is in part an effect of experience.

4. The visual cortex of the cat contains cells that fire in response to the movement of a contour (a dividing line between a light and dark area) across an appropriate area of the retina, and which are differentially sensitive to contours in different orientation (Hubel and Wiesel, 1959, 1962). These units, which were first discovered in the cortex of the adult cat, are found in newborn kittens, and are already differentiated in their function at or shortly after birth, even in the absence of patterned visual experience, although the orientation of the receptive fields is not so clear-cut as in adult cats (Hubel and Wiesel, 1963). If the kittens are reared to the age of two or three months with one eye deprived of pattern vision, contours moved across the deprived retina will not activate the cortical cells (Wiesel and Hubel, 1963). Further, this deprivation causes a partial failure of normal cell growth at a lower level in the visual system (lateral geniculate nucleus) (Wiesel and Hubel, 1963a). These observations on the electrophysiological effects of visual deprivation are compatible with the results of

behavioral studies, which show that some mammals reared without patterned visual experience are deficient in the ability to learn visual discrimination habits (Riesen, 1960) and in the ability to transfer visual pattern discriminations learned through one eye to the other eye (Riesen, Kurke, and Mellinger, 1953). The performance of visual discrimination behavior requires not only experience in the sense of visual patterns reaching the eye, but also some experience of the coordination between motor activities and the visual consequences of these activities (Riesen and Aarons, 1959; Held and Hein, 1963). This suggests that the effects of visual experience on behavior are not limited to the development of the electrophysiological mechanisms described by Wiesel and Hubel, but include developmental effects upon wider areas of behavior. Different kinds of experiential effects upon the development of behavior range from the degeneration of an already developed neural mechanism, as shown by Hubel and Wiesel,[6] through more and more specific effects, some of which must be interpreted as conventional learning (Riesen, 1961). Of this range of effects, Lorenz says:

> It is a matter of taste whether or not one choses (*sic*) to call it learning when an activity is necessary to prevent atrophy and disintegration of a physiological mechanism, but it can be regarded as adaptive modification and it may well involve ontogenetic acquisition of information. . . . These modifications . . . must, therefore, never be forgotten or overlooked in our attempts to analyze this function. On principle, however, they are no obstacle to the solution of our fundamental question concerning the provenience of the information underlying each point of adaptedness in behavior. . . . But there is little danger, with circumspect experimentation . . . and with an experimenter knowing its pitfalls, that any process of true learning, particularly classical conditioning, might pass unnoticed.

Here again, Lorenz indicates his opinion that "true learning, particularly classical conditioning" is the only kind of effect of experience on the development of animal behavior that is of serious interest to a student of such behavior.

5. The structure of the joints in the foot and leg of the domestic chick,

[6] I am embarrassed to recall that, in a review of the first edition of the book by Thorpe (1963a), I said of his attitude to this problem: "When experiment shows that some 'instinctive' act does not develop when practice is prevented, Thorpe speaks of the 'regression' of the instinct through non-use, thus preserving its 'innateness' in the face of the most direct possible evidence to the contrary" (Lehrman, 1957). The work of Hubel and Wiesel shows that I was much too abrupt in my reaction to this comment of Thorpe's. As I hope will be clear from the present discussion, at that time Thorpe and I both used the term "innate" without differentiating between different meanings that the term could have, or between the different conceptions that scientists interested in different kinds of problems could have.

and of the articulating surfaces of the foot and leg bones, depends upon the movement of these bones during their period of embryonic development. If the muscles of the embryonic limb are paralyzed either by interrupting the nerve supply or by treatment with pharmacological blocking agents, striking abnormalities develop, including complete lack of movement of the joints. The abnormalities include failure of the joint cavities to develop, distortion of the articulating surfaces, and failure of development of the cartilages and ligaments which surround the joint and bind the bones (Drachman and Sokoloff, 1966). It is thus clear that skeletal muscle contractions are essential for normal formation of the structural prerequisites for walking in these animals. Movements of embryonic muscles, which are to some extent the result of spontaneous activity of the central nervous system (Hamburger and Balaban, 1963; Hamburger, Balaban, Oppenheim, and Wenger, 1965), may also be affected during later stages by external stimuli, including stimuli arising from spontaneous movements (Carmichael, 1946). This is a borderline case in which it is not at all clear to what extent afferent inflow plays a role in determining the amount or direction of the relevant movement, but it is clear that the participation of the nervous system in the development of the normal morphological prerequisites for locomotor behavior are only illuminated by a treatment which produces a striking abnormality.

6. If embryos of the fish *Fundulus heteroclitus* are kept in magnesium chloride solutions, a small percentage of them will develop into hatchlings with only one centrally-located eye (Stockard, 1909), and these fish will apparently be able to see (Rogers, 1957). This sort of treatment, and this result, would seem to me to be the quintessence of the production of a pathology by abnormal rearing, of the kind which Lorenz asserts is of no interest to the student of adaptation to the environment. These fish do, however, suggest a couple of questions, which might provide food for thought: first, are the number and location of the eyes an adaptive character; and second, is the information about the number and location of the eyes located in the genome or in the relationship between the genome and the chemical environment? If we say that the information about the structure and location of the eyes is contained in the genome, rather than in the relationship between genome and environment, then we must be referring to the fact that different kinds of animals reared in the same environment will develop eyes of different structure and location. This again, however, means appealing to the fact that there are *differences* between animals reared in the same environment as proof that there are *differences* in the genomes. I do not see any way out of this apparent paradox except to acknowledge that statements about the genic origin of characters in complex multicellular animals are meaningful primarily when they refer to the

differences between different animals in the same environment as evidence that there are differences in the genomes.

The preceding series of examples of different kinds of modification of development, leading to different kinds of outcomes, is not at all intended to show that anything about the structure of the eyes, or of the joints, or of the visual system, or of the adrenal glands, must be "learned." It is a series of examples of rearing in abnormal environments which lead, through mechanisms of varying degrees of specificity and generality, occurring at different developmental stages, affecting growth processes with different degrees of directness, to developmental outcomes that represent interferences with the normal adaptive characteristics of the animal. All of these outcomes, however, throw light upon the manner in which those adaptive characteristics develop, and on the extent to which environmental influences may play a role in their development. The distinction between "learning" and other forms of "experience" is not sharp, although it is possible to see characteristic differences among different examples; the differences between environmental influences involving effects upon the activity of the nervous system and those not involving such effects are also not sharp, and many intermediates are possible. This is not to say that no classifications are possible, and that no distinctions can be made, among the various kinds of environmental influence. It is to say, however, that the distinction between "morphological ontogeny producing structure" and "trial-and-error behavior" producing learning (Lorenz, 1965), is not a realistic way of surveying the actual range of developmental processes that are involved in the ontogenetic origins of behavior, or of illuminating the varying processes that produce the phenotypic appearances of behavior.

To or From? The Perception of Development

Lorenz asserts that "some American psychologists" avoid the concepts of survival value and phylogenetic adaptation for no other reason than that they regard them as "finalistic." As Lorenz says, "they are not finalistic in the least. If a biologist says that the cat has crooked, pointed claws 'with which to catch mice,' he is not professing a belief in a mystical teleology, but succinctly stating that catching mice is the function whose selection pressure caused the evolution of that particular form of claws."

The concepts of adaptation and of natural selection are of course not teleological or preformationist, and Lorenz is quite wrong in asserting that Schneirla or I ever regarded them so. I believe, however, that a scientist who is interested in the analysis of development must have quite a different attitude toward some problems of causality and abnormality than that which is appropriately characteristic of a biologist who, like Lorenz, is

primarily interested in the facts of adaptation and of evolutionary variation. If the observer's perception of a developmental process is wholly dominated by his pre-knowledge of the outcome (i.e., of the adaptive form of the fully developed behavior or structure), then it is very easy for an alteration of the developmental process, caused by a change in the environment, to seem like merely a "deviation" from the "normal" course of development. It would then seem quite natural for such an observer to say that any environmental treatment that led to a maladaptive outcome was of no interest to him, since it merely consisted in the production of a pathology, and not in the illumination of a normal course of development. To such an observer, the development of the normal genome in the normal environment to the normal outcome is merely the *background* for the production of what he is really interested in: the details of structure and behavior by which the organism is intricately adapted to the details of its environment.

The investigator who wishes to understand developmental processes analytically must, however, have quite a different attitude toward the "normal." For him, the normal and the abnormal environment are simply two ways of treating the developing organism, and it is precisely by considering how the development is changed by any particular variation in the environment that he arrives at some understanding of the mechanisms of development. It would be overstating the case (but not by very much) to say that for the student of development, the normal environment and the normal path of development are no more meaningful or significant or perceptually prominent than any other environment or outcome. The reason why it would be overstating the case is that the student of development is, of course, interested in understanding the ontogenetic origin of the actual characteristics of real species, and he cannot (as Lorenz quite rightly points out) apply experimental treatments entirely at random, regardless of whether they will throw light upon the normal developmental outcome. It remains true, however, that insight into normal developmental processes comes from comparing normal and abnormal treatments and outcomes so that they are illuminated by the differences between them. From this point of view it is not at all true to say that the more abnormal a developmental outcome, the less insight it gives into the normal outcome.

One way of putting this point is that the student of adaptation and evolutionary variation often regards development as proceeding, at any stage, *toward* the functional form, since it is the functional form that is adaptive and since natural selection has acted to select genomes which, in a natural environment, produce the functional form; while for the analytic student of ontogeny, development must be seen as proceeding, at any stage, *out of* the immediately preceding stage, and as being produced by processes going on at that time, since it is *his* aim to understand the processes that create developmental change. The student of adaptation and evolution may, therefore, be talking in entirely legitimate and meaningful terms about the problem in which he is interested, while the application of the same terms and concepts to the problems in which the student of ontogeny is interested may accurately be seen as the intrusion of teleology and preformationism. It is in this sense that Lorenz's use of the concepts of adaptation in the discussion of development may be seen as "finalistic" by writers who do not in the least lack understanding of biological concepts.

CONCLUSION: SOME PROBLEMS OF COMMUNICATION AMONG SCIENTISTS

It is clear that at least some of the difficulties in the discussions of the concept of "innateness" arise from the fact that while the various writers believe, and convey to their readers, that they are arguing about matters of fact or interpretation with respect to which one side or the other must be wrong, they are in fact talking about different problems. To some biologists interested primarily in the functions of behavior and in the nature of behavioral adaptations achieved through natural selection, many developmental effects of experience seem trivial and uninteresting, and do not appear to bear upon *their* central question, of the role of natural selection in the establishment of the specific details by which the behavior of specific species is adapted to the necessities of specific environments. To the student of development, however, experiential effects, no matter how diffuse and no matter how remote from the specific details of any particular sensory discrimination or motor act, must be seen as part of the network of causes for the development of any behavior pattern or behavioral capacity to which they are relevant. Further, the rest of the network seems, to such a biologist, definable only in terms of the outcome of experiments on individual development. It ought to be possible to agree on ways of formulating the concepts with which we work so that confusing meanings will be avoided, and so that mutual misunderstandings could be minimized.

One difficulty in the way of such harmony lies in the fact that intelligent people, like unintelligent ones, resent implications that they are illiterate or incompetent, and tend to defend themselves against them. In this essay, I have not succeeded in concealing my resentment at Lorenz's repeated implication that Schneirla and I are or were ignorant of biological concepts; and Lorenz's book repeatedly expresses his sense of outrage at being reminded, as if he did not already know them, of concepts of development which no biologist would deny. It is true, however, that in my earlier contribution to this discussion, I did not deal adequately with the conceptual

problems posed by the adaptive character of species-specific behavior, and that what I have said in this essay represents what is, for me, a formulation of problems which I had not considered in detail previously. It is equally true that the formulation of the concept of "innateness" in his recent book is quite different from the concepts found in Lorenz's earlier writings, which always strongly implied developmental fixity as an essential criterion of innateness. There is, therefore, something unbecoming about my implication in this essay that I always knew what I now say, and that I am merely clarifying it for the benefit of people who could not understand it; just as there is something unbecoming in Lorenz's insistence that all criticisms of his point of view are based upon the ignorance of its critics, even while he changes some of his conceptions to meet the criticisms.

I do not think that this kind of problem can be eliminated in scientific communication, and I mention it now for no other reason than to try to make explicit something which is very often inherent in complex discussion. We do not lightly give up ideas which seem central to us, and when they are attacked, we tend to mobilize defenses against the attacks. This means restating the attacked ideas in such a form as to make them seem again convincing to an audience whose confidence in them might have been weakened by the criticism. But when we change the formulation of the ideas in such a situation, we may also be modifying the ideas themselves, in response to criticisms which really may have been leveled against weaknesses in the original formulations. The distinctions are not at all sharp or clear between restating an idea in a clearer form, modifying the idea so as to meet criticism, adding to the formulation things which were previously known but left out as unnecessary, and actually seeing new relationships and new concepts as a consequence of grappling with criticism. I think that no participant in active scholarly discussion can be absolutely sure that everything that he now says represents his long-standing knowledge, without the incorporation of any criticism, and without the inclusion of new ideas made possible only by coping with criticism. If this is a criticism of anybody's writing, it must also apply to some of my own writing in this very essay.

Lorenz believes that what students of behavior are primarily, or even solely, concerned with should be "to elucidate . . . the amazing facts of adaptedness." People interested in analytic studies of the causation and the development of adaptive behavior, however, also have other interests, which are equally legitimate, and for which the concepts derived solely from the study of function and adaptation may not be centrally useful. It is not necessary that all problems fit into the same conceptual framework. It is not required of any theory based on watching intact lower vertebrates that it explain the causes of war, the physiology of the nervous system, and *also* the mode of action of the genes; and it is not an affront to any theory to point out that there are some questions that it cannot answer because it has not asked them.

If it seems that this essay has been oriented primarily to a discussion of Lorenz's recent book, this is only because that book is the most recent attempt at a comprehensive discussion of the so-called "heredity-environment" issue in relation to animal behavior. My central aim has been, not to criticize any other point of view, but to present a positive statement of the relationships between the problems of adaptiveness and of development as seen from the point of view identified with, and best exemplified by, the late T. C. Schneirla.

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