

The Persistence of Dichotomies in the Study of Behavioral Development

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Abstract:

The inadequacies of dichotomous views of behavioral development that oppose learned and innate behavior, or genetic and environmental determinants of behavior, have long been recognized. However, they continue to exert a powerful influence on current thinking about development, often by way of metaphors that simply recast these old ideas in a more modern technical vocabulary. The idea that the information for behavior can be attributed to either genetic or environmental sources was originated by Lorenz and provides the basis for many current dichotomous accounts of behavioral development. Lorenz's "sources of information" metaphor for development is fundamentally flawed, however, as are those more recent accounts that are based on it. The alternative interactionist account of development, most clearly articulated by Lehrman, is a far more powerful and coherent theoretical framework for development, but it has not been broadly assimilated into psychology and continues to be widely misunderstood. In particular, the interactionist account does not involve a radical environmentalism, does not attribute all behavior to the effects of learning, and does not interpret development as a gene-environment interaction. The attractive simplicity of dichotomous thinking encourages its continued application to the study of development despite the fact that it is clearly inadequate to the complexities of developmental analysis.

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Article:

The reports of my death are greatly exaggerated.
~Mark Twain

One of the most popular and pervasive myths in the modern study of behavioral development is that the old distinction between learned and innate behavior has now been completely eradicated and replaced by an "epigenetic" or "interactionist" approach. What may be called the "official view" of modern developmental theory, frequently presented in textbooks of introductory psychology and of human development, is that the "nature-nurture issue" is a topic of mainly historical interest. According to this view, modern developmental theory sees all behavior as resulting from the action of both genes and the environment, having abandoned its earlier, misguided attempts to assign particular patterns of behavior to either one or the other source. Unfortunately, the appearance provided by the official view is largely an illusion: Despite a number of changes in the language in which discussions about development are typically conducted, the conceptual inadequacies inherent in the various dichotomies that pervaded the field 50 years ago are still prevalent in developmental thinking today. Terminological adjustments have allowed many writers to retain a dichotomous approach to development, while at the same time appearing to embrace the interactionist viewpoint by rejecting the older dichotomy that opposed the concepts of learned and innate behavior. Thus we find writers rejecting the learned-innate dichotomy in one paragraph, only to introduce an opposition between hard-wired and soft-wired behavior, or closed and open programs of behavior, or phylogenetic and ontogenetic sources of information for behavior, in the next. The new terminology borrows heavily from the information sciences, acquiring in the process a patina of technical respectability that obscures the continuing developmental inadequacy of the concepts to which it refers.

Unfortunately, it is often difficult to determine exactly what is meant when metaphors such as these are used in discussions of development. Those who do use them often respond to criticism by saying that the terms are only a convenient shorthand, that they are fully aware of the logic and importance of the interactionist viewpoint for understanding development, and that they (like all right-thinking developmental theorists) are sick and tired of having the nature-nurture issue periodically disinterred from its well-deserved grave. It is less often made clear what these terms are intended as shorthand for, nor is it obvious how the interactionist viewpoint is to be reconciled with the persistent (even if metaphorical) use of such dichotomies. Metaphors and shorthand are, of course, time-honored devices in scientific exposition, but they demand periodic reexamination to ensure that they continue to illuminate rather than obscure the problems they address—the road to confusion is paved with compelling but inaccurate metaphors.

The aim of this paper is to examine critically these modernized versions of the learned-innate dichotomy in the study of development, and to dispel some of the confusions and misunderstandings that seem to have arisen about the alternative interactionist approach to behavioral development. Rather than attempting to deal piecemeal with every example of dichotomous thinking in the current literature, the paper focuses on the work that provided its prototype, namely the distinction between phylogenetic and ontogenetic sources of information that was made by Konrad Lorenz in his book, *The Evolution and Modification of Behavior* (Lorenz, 1965). This book is Lorenz's response to criticisms by Lehrman (1953), Schneirla

(1956), Jensen (1961), and others of the theory of instinctive behavior that he had developed during the 1930s and 1940s. Despite the fact that more than 20 years have passed since its publication in English, Lorenz's book remains one of the clearest and most forceful expositions of the information metaphor for behavioral development. The position for which he argued has (in a number of different versions) become so widespread that it is difficult to find a more recent statement than his that does more than adopt some variation of the position as a matter of course in discussions of behavioral development. This analysis of Lorenz's book is not intended so much as a criticism of his work in particular as of a style of thinking of which his work provides a particularly good example. A later section of the paper considers the similarities between Lorenz's ideas and those of more recent authors (who may or may not have derived their ideas from his). But it is the logic of a particular kind of argument that is of primary concern, not the instantiation of that logic in the writing of any particular theorist.

THE DEVELOPMENTAL COMPONENT OF LORENZ'S THEORY OF INSTINCT

Lorenz's Early Theory

In order to understand the way in which Lorenz arrived at his dichotomy between phylogenetic and ontogenetic sources of information for the development of behavior, it is important to look at the historical context in which his 1965 book was written. During the 1930s and 1940s Lorenz, in collaboration with other European biologists, especially Nikolaas Tinbergen, had developed an important and highly influential theory of instinctive behavior (Lorenz, 1935 [translated as Lorenz, 1937a and 1957a]; Lorenz, 1937b [translated as Lorenz 1957b and 1970]; Lorenz & Tinbergen, 1938). This theory, which became the mainstay of the emerging science of ethology, included as one of its components a strict distinction between two kinds of behavior: *instinctive behavior*, which was stereotyped, species-specific, independent of experience, and determined by the genes; and *learned behavior*, which was variable and depended on the experience of the individual. These two kinds of behavior were seen as quite independent of one another, admitting no intermediates—if a particular pattern of behavior appeared to be a blend of learning and instinct, that was only because the behavior had not yet been resolved into its elementary learned and instinctive components.

An important task for the ethologist was to determine which of the many behavior patterns exhibited by an animal were learned and which were instinctive, and for Lorenz the methodology of choice was the *deprivation experiment*. In a deprivation experiment, an animal is reared from an early age in circumstances that deprive it of the opportunity to learn anything about the behavior under study. It is prevented from practicing the behavior, and from observing or imitating the behavior of other members of its species. If the behavior normally involves a response to a specific environmental stimulus (and instinctive behavior, in classical ethological theory, was thought to be normally "released" by a specific "sign-stimulus" or "social releaser"; see Lorenz, 1937b; Tinbergen, 1951), then the animal is denied any exposure to that stimulus. At the appropriate age, when the behavior would normally be seen, the animal is given the opportunity to demonstrate the behavior. If the behavior appears in its normal, species-typical form, then it is diagnosed as instinctive; if the behavior does not appear, then it is diagnosed as learned. (Intermediate cases, in which the behavior appeared, but in an abnormal form, were thought to be due either to poor experimental design, or to the fact that the elementary units of behavior had not been properly identified.) For example, if a young pigeon is reared in a cage that is too small to allow it to stretch its wings and practice the movements of flight, and is not

allowed to observe other birds flying, it will nonetheless fly normally when it reaches the appropriate age (Grohmann, 1939). Hence, flight in pigeons is an instinctive behavior. Sometimes the learned-innate dichotomy could not be made for entire behavior patterns, but would still apply to aspects of a behavior pattern. Eibl-Eibesfeldt (1956) reared squirrels without the opportunity to open hazelnuts. When the animals were given the nuts to eat, the motor patterns of gnawing the shell were identical to those of normally reared, experienced animals. However, only with practice did the deprived animals orient their gnawing so as to open the nuts efficiently. Hence, in squirrels the motor patterns involved in gnawing are instinctive, but the orientation of gnawing is learned.

Given the conceptual dichotomy between instinctive and learned behavior, the logic of the deprivation experiment is compelling: Deprive an animal of the opportunity to learn, and the only behavior that will develop is what is instinctive or innate. Behavior was thus seen to derive from one of two sources: from the environment if learned and from the genes if innate. If the first of these sources is withheld (as the deprivation experiment aimed to do), then only the second will be available.

Lehrman's Critique of Lorenz's Early Theory

Lorenz's theory of instinct was largely ignored by American psychologists until it received a cogent critical analysis in a justly famous paper by Daniel Lehrman (1953). Earlier developmental theorists such as Kuo (1921) and Carmichael (1925) had attacked the dichotomy between learned and innate behavior, but, perhaps because of the tremendous influence that Lorenz's theory was exerting in the growing field of ethology, Lehrman's criticism had a far greater impact on developmental thinking than did these earlier writings. Lehrman's critique had several components of which I will consider only those that concern the developmental implications of Lorenz's theory. Lehrman pointed out that Lorenz's view of instinct had nothing to say about the development of behaviors that are not learned. If a behavior does not depend on practice, trial-and-error learning, observation, or imitation, then for Lorenz that behavior is innate and its origin is to be found in the genes. But as Lehrman argued, attributing behavior to the genes does not solve the problem of its development, it simply refuses to address the problem. The genes clearly do not *contain* behavior, so the developmental question of how we get from the genes to behavior remains unanswered. Lehrman suggested that a more productive way to look at behavioral development in terms of the continuing interaction that occurs between the animal and its environment as development proceeds. The behavior characteristics whose development we seek to understand emerge from this interaction, and so we should aim to analyze how the animal and its environment interact in the course of development. Note that for Lehrman, development involves an *animal-environment* interaction, not a *gene-environment* interaction, as is so often supposed. The distinction is crucial, and I shall return to it later.

To perform this analysis, Lehrman proposed a methodology that seems superficially similar to the deprivation experiment, but that is in fact radically different, both in conception and in interpretation—the selective rearing experiment. A *selective rearing experiment* aims to test a specific hypothesis about the contribution of a particular aspect of the environment to the development of a particular behavioral characteristic, not to distinguish between two different categories of behavior. If we suppose that the development of song in male white-crowned sparrows depends on hearing species-typical song in early life (Marler, 1970; Petrinovich, 1985),

we test the hypothesis by selectively withholding that experience, and examining the effect of that treatment on song development. The aim is *not* to determine whether song is learned or innate, but to determine whether (and how) exposure to song contributes to the normal course of song development.

The main point of Lehrman's argument was not to take a stand on the issue of whether, or how much, behavior is due to the environment as opposed to the genes, but rather that any such stand simply reflects a misunderstanding about the nature of development. *All* behavior depends somehow on the interaction between the animal and the environment, just as *all* behavior depends somehow on the activity of the genes. The problem was that in 1953 nothing was known about how the genes act in development (and not much of relevance to behavioral development is known today), so Lehrman could make little contribution to unraveling that aspect of the developmental problem. The animal-environment interaction, however, is readily accessible to experimental investigation, so Lehrman proposed that we investigate it. It is ironic that to many ethologists, Lehrman came to represent an extreme environmentalist position on the nature-nurture issue, whereas in fact he argued that the issue itself is simply misconceived.

Lorenz's Response to Lehrman, and the "Sources of Information" Metaphor

Lehrman's criticism of Lorenz was supplemented by other American psychologists such as Schneirla (1956) and Jensen (1961), and by some European (mainly British) ethologists, such as Hinde (1955). Lorenz vigorously defended his position (Lorenz, 1956, 1965; see also Eibl-Eibesfeldt, 1961) and in the process gave his argument a new twist. He acknowledged that it might be unwise to speak of *behavior* itself as being due either to the genes or to experience, but contended that it was still possible to speak of the *information for behavior* as being supplied in development by one or the other of these two sources. He vigorously attacked his critics (especially Lehrman and Jensen) who, he asserted, had simply failed to recognize that the issue of central importance to any biological analysis of behavior is the question of adaptedness: How is it that behavior is adapted to the requirements of the animal's environment? Adaptedness, Lorenz said, requires information about the environment, and that information can come from only two sources. Either it is provided by the evolutionary process of natural selection, in which case it is *phylogenetic information*, encoded in the animal's genes (as a "genetic blueprint"; see further below), or it is provided by the developmental processes of learning, in which case it is *ontogenetic information*, available in the environment of rearing. The major question for a developmental analysis is to determine the source of adaptive information for the behavior, or aspect of behavior, under study, and the deprivation experiment enables that question to be answered. Deprivation rearing allows the experimenter to exclude ontogenetic sources of information; thus, whatever adaptively organized behavior develops under such conditions must be due to phylogenetic information encoded in the genes. It is the latter behavior, Lorenz argued, that ethologists refer to by the term "innate."

In discussing the deprivation experiment, Lorenz was careful to draw a sharp distinction between two kinds of result from deprivation rearing. First is the case in which the experiment has successfully excluded a source of ontogenetic information, allowing a behavior to be diagnosed as either learned or innate. Second is the case in which a behavior fails to develop due to the effects of "bad rearing." Lorenz pointed out that even innate behavior requires certain environmental conditions in order to develop properly. If we do not feed an animal a proper diet,

it will sicken and die, and so its behavior will not develop normally. But we cannot on that account say that the behavior is learned: It may still be innate, but the environmental conditions necessary for its maturation have not been provided. The concept of maturation plays an important role in Lorenz's later theory of instinct, as it does in other developmental theories that employ the sources-of-information metaphor. Maturation (usually "strictly determined maturation" in Lorenz's writing) is the developmental mechanism by which genetically encoded phylogenetic information becomes translated into behavior. However, the information that gets translated in the process of maturation comes from the genes; the environment provides essential support for that process, but contributes no information to it. The details of the maturation process are, to Lorenz, relatively uninteresting for the study of behavior. They lie in the province of experimental embryology and can be ignored in the pursuit of more interesting behavioral questions about the sources of information for behavior.

However, Lorenz's sources-of-information metaphor is deeply flawed, even granted that he, like all scientists, is at liberty to declare an interest only in certain questions about the phenomena he studies. I turn now to examine that metaphor in its own terms, after which I shall consider whether its inadequacies extend to other versions of the metaphor that are to be found in more modern writings on development.

INFORMATION IN DEVELOPMENT AND ITS SOURCES

The appeal of terms like *information*, *blueprint*, *program*, and *hard-* or *soft-wiring* in discussions of development is that they lend an air of technical precision to the discussion. Unfortunately, they refer to concepts that are in fact very imprecisely understood. When a computer scientist or communications engineer speaks of information being encoded in a program, or being input to a program during its execution, the meanings of those terms are unambiguous and they can always be translated into a precise (even if cumbersome) specification of exactly what is happening. When the same terms are used by a developmental theorist (especially when talking about behavior) no such precise specification exists and we must ask whether the (necessarily) metaphorical use of the terms is helpful or misleading.

The Definition of "Information"

Lorenz does not provide a definition of his concept of information, but a precise definition of the term is available in communication theory from the work of Claude Shannon (Shannon & Weaver, 1949) and Norbert Wiener (1948). The Shannon—Wiener concept of information has been borrowed by many psychologists and biologists who have found it of broad applicability in the life sciences. It is not necessary to explicate any of the mathematical details of information theory here; what is required is simply an understanding of the idea that is formalized in the mathematics.

Information is fundamentally a matter of the alternative states of two systems that are in communication (that is, that interact with one another). One of the systems, called the *sender*, influences the other system, called the *receiver*; the physical event that makes possible the interaction between the two systems is called the *signal*. So, to take an example from the study of animal communication, a vervet monkey can communicate the presence of a leopard (a potential predator) by producing a particular vocalization (Seyfarth, Cheney, & Marler, 1980). Other animals respond to this signal by running to the tops of trees, an appropriate response for

monkeys avoiding leopards. Here a sender (the vocalizing monkey) communicates information to a receiver (another monkey in the group) by transmitting a signal (the vocalization). The fact that information is communicated in that situation depends critically on the existence of alternative signals that might have been sent but were not. Had the signaling animal sighted a martial eagle rather than a leopard, it would have given a different call, and the response of other group members would have been different (they would have left the trees and hidden in the dense undergrowth); sighting a snake would have produced yet a third call, and a different response (mobbing). Without the existence of these alternatives (and others, including signals having nothing to do with warnings about predators), the situation would not involve the transmission of information at all. The effect of the transmission of information is to set in train one complex sequence of events (resulting in the other group members running into the tree tops) rather than some other sequence of events (resulting in the other animals hiding in the bushes, for example). The only way in which an observer of the situation can determine whether or not information is communicated is by observing that transmission of a specified signal produces one outcome rather than another. The transmission of information may thus be defined as *the production of one out of several alternative states of affairs in a system (the receiver) because of the influence (via the signal) of another system (the sender)*.

Ontogenetic Sources of Information for Behavior

Consider now the way in which the concept of information is to be analyzed in the developmental metaphor of the environment providing a source of ontogenetic information for behavior. The source of information (the sender) is the environment, the receiver is the developing animal, and the signal is whatever aspect(s) of the environment influence the developing animal. We can decide whether information is transmitted between the environment and the animal by determining if a change in the environmental influence on the animal (i.e., a change in the signal) produces one developmental outcome rather than another. If we change some aspect of the environment, and that change alters the outcome of development, then the aspect that we changed provides a source of information for the developing animal; if our manipulation of the environment does not affect development, then the aspect we changed does not provide a source of information. Thus the metaphor of the environment as a source of ontogenetic information for behavior can be given an interpretation that is consistent with the formal definition of information. Unfortunately, that interpretation is completely at odds with the theoretical role that Lorenz would assign to the metaphor in his analysis of development.

Recall that Lorenz maintains a strict (and theoretically essential) distinction between experimental manipulations of the environment that reveal a source of ontogenetic information (a correctly executed deprivation experiment) and superficially similar manipulations that simply prevent the maturation of an innate behavior ("bad rearing"). Both manipulations reveal that the environment provides a source of information to the developing animal, because both produce a change in the outcome of development, yet Lorenz insists that the interpretations of the two experiments must be kept theoretically distinct. How is that distinction to be maintained? It cannot be maintained by appeal to the relative nonadaptiveness of the different outcomes of development, because the lack of a "learned" behavior pattern would not seem (by virtue of the pattern's normally being learned) any more or less of an adaptive handicap than the lack of an "innate" pattern. The distinction might be maintained by arguing that only when the alternative developmental outcomes are normally to be found among members of the species are we entitled

to say that the environment provides a source of ontogenetic information, by selecting among those alternative outcomes. Although the question of whether development normally is variable or invariable is an important one for developmental theory to address (Johnston, 1982), it does not help us to disentangle this particular puzzle. The futility of arguing in this manner can best be illustrated by way of a hypothetical example that provides a *reductio ad absurdum*. At present, human infants growing up in different societies may learn any of several hundred languages, depending on which one is spoken in their natal linguistic environment, and thus language development in humans has a wide range of normal outcomes. By the criterion under discussion, language is learned, and the environment therefore provides a source of ontogenetic information. Suppose that some strange catastrophe eliminated all of the human species except for those groups that currently speak only Italian. After the catastrophe, language development in humans would have only a single outcome, and any alternative outcome produced by experimental manipulations would, by definition, be nonnatural. Would we therefore be required to argue that whereas language was "learned" before the catastrophe, after the catastrophe it became "innate"? The argument from natural variability would have us do so, but at the cost of a bizarre reinterpretation of what is meant by the terms "learned" and "innate." They would become exactly synonymous with the terms "variable" and "invariant," respectively, and would thus be purely descriptive terms with no explanatory content at all. So although an appeal to the naturalness or nonnaturalness of the alternative outcomes of development is available as a way of saving the distinction on which Lorenz insists, it can then be employed only at the cost of eliminating the explanatory capability of any development theory that uses the terms.

Is there, then, *any* principled way in which the distinction can be maintained? I think not. In making the distinction, Lorenz (1965, chap. 7) appeals frequently to the knowledge that an experienced ethologist brings to the developmental study of any animal's behavior. The suitably trained ethologist will, Lorenz implies, know intuitively when ontogenetic information has been withheld and when the animal has simply suffered the effects of bad rearing. That criterion, of course, is no criterion at all. It merely allows the ethologist to make *ex cathedra* pronouncements on what is learned and what is innate in behavior, and to dismiss the criticisms of those who disagree on the grounds that they lack the necessary insights into animal behavior. Consider again the results obtained by Eibl-Eibesfeldt (1956) from his studies of hazelnut opening by squirrels. Lorenz interprets the results as showing that orientation of gnawing is learned, whereas the motor patterns of gnawing are innate. The deprivation experiment successfully withheld ontogenetic information for the acquisition of appropriate orientation. But what is to prevent Lorenz, if he prefers, from arguing that the orientation of gnawing, like the motor patterns themselves, is innate, and that the "bad rearing" induced by Eibl-Eibesfeldt's experimental conditions blocked the normal maturation of that innate component of behavior? Without some principled set of criteria for making such decisions, the identification of ontogenetic sources of information for the development of behavior becomes a matter for the investigator's whim, not for scientific inquiry.

When a reasonably rigorous definition of information is applied to the problem of identifying sources of ontogenetic information (see above), the program of research that naturally follows is precisely that recommended by Lehrman (1953, 1970) and Jensen (1961). That is, we manipulate some aspect of the environment (selected to test a specific hypothesis about how behavior develops) and, using appropriate control groups, determine whether the manipulation affects the

course of development. If it does, then an environmental influence has been identified, and our understanding of development in that species correspondingly advanced. If the manipulation does not affect the outcome of development, then the experiment has produced a negative result, with all the problems of interpretation that such results usually involve. If we wish, we can describe aspects of the environment that influence development as sources of information for behavior, a description that accords with the formal definition of information, although it contributes nothing further to our understanding of the situation. The decision whether to talk about "environmental influences on development" or "sources of information for behavior" is purely a terminological one; it implies no attempt to classify the environmental components that affect development into informative and noninformative ones.

Often, the relationship between the aspect of the environment that influences development and the behavior whose development is affected may not be as obvious as in the case of learning. If an animal learns what food to eat by trial and error, or by watching other animals eat and imitating them, then the relationship between experience and the behavior of food selection is obvious and straightforward. But suppose we find, as Gottlieb (1978, 1980, 1981) has shown, that in order for a duckling to develop the normal sharp preference for the maternal call of its own species, it must hear either its own or siblings' embryonic calls. Now the relationship between experience and subsequent behavior is less obvious and does not meet the usual criteria for learning. Nonetheless, such non-obvious dependencies (Gottlieb, 1980, 1981) are an important part of the animal-environment interaction by which development takes place. Recognizing their existence and importance is an important step towards eliminating the dichotomous approach to behavioral development, and they are further discussed toward the end of this article.

Phylogenetic Sources of Information for Behavior

Given all of these criticisms of Lorenz's concept of ontogenetic information for behavior, what is to be said about his opposing concept of phylogenetic sources of information? The weaknesses of the former concept must call the latter in question as well. Since the two concepts are meant to provide exhaustive and mutually exclusive developmental explanations for behavior, any ambiguity or imprecision in one of them must necessarily produce a corresponding ambiguity or imprecision in the other. But there are other problems with the concept of phylogenetic information for behavior as well.

In Lorenz's theory, phylogenetic information is provided by natural selection and is encoded in the genome as a genetic blueprint. In the course of development, that blueprint unfolds by way of strictly determined maturation (what Gottlieb, 1976, calls predetermined epigenesis), giving rise to phylogenetically determined ("innate") aspects or components of behavior. For such aspects of behavior, maturation provides a passive conduit by which information in the genes "unfolds" in the course of development into behavior. The metaphor of the genetic blueprint (or genetic or developmental program) has become increasingly popular as a way of maintaining a dichotomous view of behavioral development without using the terms "learned" and "innate." It seems to allow the attribution of behavior directly to the genes, without implying the preformationist view that behavior itself is present in the genes. However, it does so only at the cost of seriously misrepresenting the nature of genetic involvement in development. The idea of a genetic blueprint for behavior implies that behavior is directly represented in the genes, even if

it is not directly contained in them. That is, it implies that there are elements of the genome that stand in a one-to-one relationship with elements of behavior. Without such a one-to-one relationship, it would not be possible to identify certain aspects of behavior as due solely to information contained in the genes. But our understanding of genetic activity simply will not permit a relationship of that kind between genes and behavior (Oyama, 1982, 1985). The only information that can accurately be said to be directly represented in the genes is the sequence of amino acids that constitutes the primary structure of proteins. Once the amino acid chain has been synthesized, all further development of the phenotype results from an interaction between the phenotype and the environment. Even the three-dimensional structure of protein molecules, which gives them their functional specificity, cannot be described as "encoded in the genes," because it depends on aspects of the intracellular environment such as temperature and pH. Between amino acid sequences and behavior is a long and tortuous developmental route, most of whose details are at present unknown. We know that proteins and other cellular constituents combine somehow to give nerve cells their characteristic properties, that cells somehow interact to give rise to nerve circuits with particular functional characteristics, that those circuits somehow give rise to certain kinds of behavioral activity, and that all of these steps somehow involve the contribution of various aspects of the environment (Hofer, 1981; Stent, 1981). The metaphor of a genetic blueprint that directly specifies anything about behavior cannot possibly be maintained in the face of such developmental complexity. Further discussion of its conceptual inadequacies is provided by Oyama (1982, 1985).

The fact is that we know very little about how the genes contribute to the development of behavior, and what we do know suggests that their involvement, although critically important, is extremely indirect. Stent (1981) suggests that the genes should be seen as initiating a "cascade of pleiotropic effects" that involves a complex of epigenetic interactions among gene products (i.e., aspects of the phenotype) as well as between those products and the environment. The genes may influence this sequence of events but they do not control it. Certainly they do not specify any of its behavioral outcomes.

Stent suggests an analogy between the epigenetic process of development and the ecological process of succession, in which an area of bare earth becomes colonized by a complex community of plants and animals. Succession occurs in a regular and predictable fashion, with different species appearing, establishing themselves, and then disappearing in a well-defined sequence. This regular sequence of events depends on interactions between the successive organisms and their environment (including such fundamental aspects of the environment as climate and soil type), as well as among the various organisms that are participating in the succession. It is the interactions themselves that produce the regularity; there is no separate source of information (an "ecological blueprint") controlling the sequence of events. The nature of succession is importantly influenced by such things as the chemistry of the soil and the availability of appropriate seeds at various times in the succession, all of which contribute to the orderliness of the sequence, although they do not determine it. Viewing development in the light of Stent's metaphor may help us to see that both the genes and the environment contribute to the developmental regularities we see, although neither alone specifies any aspect of the process.

Stent's metaphor is, of course, only a metaphor and not an explanation for development. However, the power of metaphors lies in their ability to direct our attention to promising lines of

inquiry, and to suggest new and fertile ways of conceiving complex phenomena. The analogy that Stent draws is at least compatible with what we know about the role of genes in development in a way that Lorenz's sources-of-information metaphor is not. Perhaps, then, it will help to illuminate the contribution of the genes, even if it does not directly explain it.

DICHOTOMIES IN THE MODERN STUDY OF BEHAVIORAL DEVELOPMENT

The preceding critique shows that Lorenz's metaphor of two sources of information for behavior is entirely inadequate for guiding the analysis of behavioral development. The idea that ontogeny and phylogeny provide two separate sources of information for behavior requires us to make distinctions among environmental influences on development for which there is no apparent justification, and the concept of a genetic blueprint for behavior cannot be maintained in the face of our growing understanding of gene action in development. Neither the original distinction between "innate" and "learned" behavior, which was so effectively criticized by Lehrman (1953), nor the revised dichotomy between phylogenetic and ontogenetic sources of information for behavior makes a useful contribution to our understanding of development. Nonetheless, these dichotomies, and others derived from them, continue to have a widespread and powerful influence in modern thinking about behavioral development.

Learned Versus Innate Behavior

Despite the widespread acknowledgment that Lehrman's (1953) criticism of Lorenz provides cogent and compelling grounds for abandoning the learned-innate dichotomy and the concept of instinctive behavior as guides to developmental analysis, the distinction between the two kinds of behavior persists in current writings on behavioral development. Textbooks of introductory psychology and human development continue to use the terms "learned" and "innate," even as they often acknowledge the inadequacies of the concepts that those terms represent. The following quotations are taken from five such textbooks. They are randomly selected, in the sense that the books were readily available on my bookshelf while I was writing this article; certainly I made no attempt to search for texts containing especially egregious usage.

In discussing the factors that influence animal behavior, Bootzin, Loftus, and Zajonc (1983) write:

No single influence can account for a particular behavior pattern. Genes, maturation, environment, and experience interact in almost every case. By examining the roles of inheritance, environment, and learning, research into animal behavior provides insight into the particular behavior patterns of a species. (p. 159)¹

The "almost" is unfortunate, but the general point of view being expressed is a reasonable one. However, the very next section, which is titled "Innate Factors that Influence Behavior," begins:

The more complex a behavior, the more likely it is generally that the behavior has been acquired through experience. No one would expect that reading and doing calculus are innate, but we would expect nursing to be an innate behavior. (p. 159; see Footnote 1)

¹ From *Psychology Today* (p. 159) by R. R. Bootzin, E. F. Loftus, and R. B. Zajonc, 1983, New York: Random House. Copyright 1983 by Random House, Inc. Reprinted by permission.

Zimbardo (1985), discussing emotion in another introductory textbook, writes:

But where do emotions originate? Are we born with them or are they learned? Evidence that emotions are innate is provided by the fact that all infants show similar emotional expressions at birth or soon after [p. 295]... [Ekman, Levenson, & Friesen, 1983] hypothesize that the connections between facial-muscle emotional expressions, the motor cortex, and the hypothalamus are "hardwired," while interpretation of emotional experience depends on learning. (p. 297)²

Papalia and Olds (1985) introduce their chapter on learning and memory with a section that includes the following statements:

Instincts are relatively complex patterns of behavior that are biologically determined and usually important for species survival. All members of a particular species show this instinctive behavior. One swallow, for example, does not stay "home" while all the others migrate to Capistrano every year at some genetically programmed signal.... [Learning] specifically excludes any ability or skill that is attained by *maturation*, the process by which biologically predetermined patterns of behavior unfold, more or less on schedule. (p. 158)³

H. Gleitman (1981), in his widely respected introductory text, under the heading "Innate Factors in Perceptual Organization," asks:

How can we discover which aspects of perceptual organization (if any) are innately given? In some organisms, important features of the perception of space are apparently built into the nervous machinery. (p. 237)⁴

Later, discussing the study of animal behavior under the heading "Fixed- action patterns: Innate or acquired?" he writes:

What is the basis for the belief that fixed-action patterns have a genetic basis? One line of evidence comes from the fact that certain stimulus releasers provoke the relevant response on the very first occasion the animal is exposed to them... The same point is made by *deprivation experiments* in which animals are raised in specially restricted conditions. (p. 419)⁵

Finally, Nash (1978), in a biologically oriented textbook on developmental psychology, concludes that:

In certain species, and perhaps in all species in certain circumstances, innate behaviors may have advantages over learned ones.... The relationship between innate and acquired behaviors is illustrated by circus animals whose innately characteristic behavior forms the basis of the "act" [p. 83].... The main purpose of [this] chapter is to review the "New Look in Instincts" and to insist that whatever the objections to the theory in other contexts it [instinct] is a useful concept to the developmentalist (p. 91)⁶

² From *Psychology and Life* (11th edition, pp. 295 and 297) by P. G. Zimbardo, 1985, Glenview, IL: Scott, Foresman. Copyright 1985 by Scott, Foresman & Co. Reprinted by permission.

³ From *Psychology* (p. 158) by D. E. Papalia and S. W. Olds, 1985, New York: McGraw—Hill. Copyright 1985 by McGraw—Hill, Inc. Reprinted by permission.

⁴ From *Psychology* (p. 237) by H. Gleitman, 1981, New York: Norton. Copyright 1981 by W. W. Norton & Co., Inc. Reprinted by permission.

⁵ From *Psychology* (p. 419) by H. Gleitman, 1981, New York: Norton. Copyright 1981 by W. W. Norton & Co., Inc. Reprinted by permission.

⁶ From *Developmental Psychology: A Psychobiological Approach* (2nd ed., pp. 83 and 91) by J. Nash, 1978, Englewood Cliffs, NJ: Prentice—Hall. Copyright 1978 by John Nash. Reprinted by permission.

Although textbook authors must often gloss over some finer theoretical points in writing for their scientifically naive audience, these passages suggest that many students are being taught a fundamentally inadequate view of development at the beginning of their psychological education. This need not be done (e.g., Hofer, 1981), but it reflects a continued and widespread acceptance of the learned-innate dichotomy that pervades even the professional literature on behavior and development.

For example, the concept of a "sensory template" plays an important role in the study of bird song. A template is a (presumably) neural structure containing a model of the species-typical song against which a songbird can match its vocal output. The fact that birds deafened just before the onset of singing do not produce normal song is usually taken as strong evidence in favor of the sensory template hypothesis (Konishi, 1965). The properties of the template, and especially the dependence of its development on hearing song early in life, have attracted a great deal of interest in the psychobiological literature, especially in the work of Marler and his colleagues (Marler, 1976). Recently, Marler and Sherman (1983) published important new evidence about the sensory template in two species of sparrow, and introduced their article in the following terms: "The two most obvious means for exerting genetic control over the structure of a vocalization are by inherited patterns of motor outflow from the brain to the sound-producing organs or by innate auditory 'templates' to which an organism would match its own voice.... The concept of innate auditory templates, modifiable through experience, is the focus of the present study" (Marler & Sherman, 1983, pp. 517-518). The literature on song development, which constitutes a large and important area within developmental psychobiology, is full of references to innate song, or innate aspects of song. For example, Kroodsma and Pickert (1984, p. 395) write that "in the perching birds (Passeriformes), the songs of some sub-oscines are innate ... in *sharp contrast* to the oscines, where vocal learning is the rule" (emphasis added; see also Kroodsma, 1984). Grant (1984, p. 89), reporting the results of a field study of song variation in Darwin's finches, concludes that "songs are probably learned and not genetically inherited." Rowley and Chapman (1986, p. 1) urge that "since ... behaviour is part innate and part learned it is important to recognize those aspects that have been transmitted genetically and those which have been acquired through the individual's experience of life."

Other studies of animal behavior perpetuate the learned-innate dichotomy. Fugle, Rothstein, Osenberg, and McGinley (1984, p. 90) mention in their discussion of the communicative significance of the white crown stripe in white-crowned sparrows that they are "unable to say whether the association between the crown signal and dominance is learned ... or whether it is genetically controlled." Moltz (1984, p. 287) describes the maternal pheromone in rats as "a stimulus whose attractiveness is innately based during one stage of development and experientially derived at a later stage."

The literature on human development also makes use of the concept of innateness. For example, Eimas (1985, p. 46), reviewing recent work on speech perception in human infants, writes that they "are richly endowed with innate perceptual mechanisms, well adapted to the characteristics of human language, that prepare them for the perceptual world they will encounter."

All of these quotations were written by professionals in the study of behavior and/or development, many of whom are widely recognized as established leaders in their respective

fields of research. All but one (Moltz's book chapter) were published in leading journals, and were presumably reviewed by other professional researchers before publication. Quotations such as these (which could be multiplied many times if space permitted) indicate that many modern students of behavioral development are quite comfortable with the distinction between learned and innate behavior. It is possible in some cases that writers who use these terms today mean something different by them from what was meant by the classical ethologists who first applied the terms systematically to the analysis of behavior. For example, "innate" is sometimes used to mean "present at birth" (i.e., congenital), or "unlearned" (without the accompanying connotation of being determined by the genes), or "invariant," or "resistant to environmental modification." All of these would be descriptive uses, without any implied explanatory content. However, the term has been used for so long in the study of development as an explanation of behavior (i.e., to refer to the determination of behavior by the genes, or by genetically encoded information), that any change to a new, descriptive use is bound to lead to confusion. The terms "innate" and "instinctive" carry too many extra connotations, many of them with impressive historical lineages (Diamond, 1971, 1974), for them to be used successfully as theoretically neutral descriptive terms. Such a redefinition is as ill-advised as, for example, starting to use the term "reinforcement" as a descriptive term to mean simply "any consequence of behavior," while trying to deny the explanatory implication that the consequence has some effect on the subsequent production of behavior. The possibility of redefinition notwithstanding, many authors who refer to innate behavior do so with the clear implication that the behavior is genetically determined, often, indeed, using that phrase directly (see several of the quotations above).

The supposedly eradicated dichotomy between learned and innate behavior appears, therefore, to be alive and well in the behavioral sciences. Furthermore, its influence has been buttressed by a number of related metaphors, some of which are also represented in the preceding quotations, and all of which derive from Lorenz's distinction between ontogenetic and phylogenetic sources of information for behavior.

Closed Versus Open Programs of Development

In addition to these continued references to innate behavior, another, increasingly widely defended, approach is to speak, as Lorenz (1965) did, of the information for behavior being innate, rather than the behavior itself. The tendency to appeal to the concepts of phylogenetic information, genetic blueprints, or genetic programs of development is especially marked among those whose interests in development are closely allied with evolutionary interests in behavior. In one of the most influential recent statements of this point of view, Mayr (1974) distinguished between closed and open genetic programs for behavior. The distinction hinges on whether the program allows for "appreciable modifications during the process of translation" into behavior (Mayr, 1974, p. 651). If it does, then the program is an open one; if not, then it is closed. In discussing the characteristics of behavior controlled by closed genetic programs, Mayr lists (p. 653) several that were used to diagnose instinctive behavior by the classical ethologists: stereotypy, utility as a taxonomic character, appearance in naive individuals, and insensitivity to environmental modification. Mayr points out that behavior is not controlled directly by the genetic program, but by "a behavior program in the nervous system which resulted from the translation of the original genetic program" (Mayr, 1974, p. 651), and "translation," in this context, seems to mean

the same thing for Mayr that "strictly determined maturation" did for Lorenz. Mayr points out (p. 652) that open programs can be seen as possessing "slots" into which the environment inserts information during development; the characteristics of those slots is determined by the program, and hence by the genes. In the same way, Lorenz (1965) spoke of the importance of the genetic blueprint for determining how ontogenetic information will be incorporated into behavior in the course of development. Mayr's concept of the genetic program suffers from all the theoretical inadequacies of Lorenz's concept of the genetic blueprint, but it has been embraced with enthusiasm by many developmentalists.

A serious problem is that Mayr's formulation can be, and often is, taken to imply that one can substitute the terms closed and open programs of behavior for innate and learned behavior, and then speak usefully about development. The danger of using the terms in this way can be seen in Mayr's own evaluation of the development of species identification in nest parasites such as the European cuckoo or the cowbird. Because the young of these birds are reared by members of another species, Mayr argues (p. 652) that "clearly in this case the program for species recognition ... was contained completely in the original fertilized zygote." But as West and her colleagues have shown (West, King, & Eastzer, 1981), experience plays an important role in the development of species recognition mechanisms in the cowbird, albeit in a manner unlike anything that might have been expected. The willingness to assign information for development to a genetic program seems to lead inevitably to a belief that development is thereby explained, with the result that important aspects of the animal-environment interaction that actually produces development go unanalyzed.⁷

Recently, Lumsden and Wilson (1981) have proposed a variant on the theme of open and closed programs of development in their concept of an epigenetic rule. They define an epigenetic rule as "any regularity during epigenesis that channels the development of ... [a] trait in a particular direction. Epigenetic rules are ultimately genetic in basis, in the sense that their particular nature depends on the DNA developmental blueprint" (p. 370). Lumsden and Wilson are far more willing than most authors to attribute phenotypic characteristics to the unfolding of innate information and, as the quotation above indicates, they readily attribute any regularity in developmental outcomes to the influence of genetic information. The tendency to take developmental invariance in a trait as license to speak of its "genetic determination" is very widespread, and seems to be an important reason for the persistence of dichotomous thinking in the study of behavioral development. I shall return to this point in a later section.

Biological Constraints and Predispositions

One of the most active areas of research in the field of animal learning for the past 15 years has concerned the issue of biological constraints on animal learning (e.g., Shettleworth, 1972; Johnston, 1981; Domjan & Galef, 1983). In brief, the idea of biological constraints on learning is that species may be predisposed to learn in certain ways rather than in others; for example

⁷ Unfortunately, King and West (1983) are in danger of perpetuating this error when they describe the female cowbird's recognition of the male's song as being controlled by a "closed program" because changing the female's experience with song does not appear to modify her preferences. The details of the animal-environment interaction that give rise to this capability remain to be explicated; King and West's (1983) data provide only negative evidence that it does not depend on prior exposure to song. More recent data suggest that Females' preference for song may indeed be modified by experience. See King and West (1987).

(Garcia & Koelling, 1966), to associate certain cues and consequences (e.g., tastes and illness) readily, while failing to associate others (e.g., tastes and shock). The nature of the constraints that determine a particular animal's learning ability, it is argued, reflect the species' evolutionary adaptation to its natural environment (in which taste and illness might often be associated, but taste and shock rarely, if at all). Thus, the argument goes, what an animal can learn (or how readily it can learn it), is determined by constraints and predispositions that are "biologically given"; or, to put the same idea in other terms, that are specified by information coded in the animal's genome. The particular learning that goes on within the constraints, on the other hand, is determined by information provided by the environment. This restatement of the concept of biologically constrained learning in terms of genetically coded information may seem slightly presumptuous, because those who use the concept have not generally given any explicit consideration to how those constraints arise. However, the interpretation that biological constraints on learning are equivalent to Lorenz's "phylogenetic information for behavior" is quite compatible with the writings of many recent authors. For example, discussing the tendency of rats to learn more readily to go to different places for food reward on successive trials than to the same place, Olton and Schlosberg (1978, p. 610) suggest that "rats are naturally predisposed to follow a win-shift strategy." In a similar context, Haig, Rawlins, Olton, Mead, and Taylor (1983, p. 337) argue that rats have "an inherent predisposition to follow a particular strategy" of foraging behavior. Schwartz (1984) summarizes his discussion of the literature on constraints on learning in the following terms:

A genetic blueprint constrains how, what, and when organisms will learn. The result of this blueprint is many specialized learning processes rather than a few general ones. The blueprint pretunes organisms to the demands of their environments so that they will be able to learn rapidly and effectively just what they need to survive. (p. 511)⁸

Schwartz uses almost exactly the same terminology as Lorenz (1965, p. 18), who urged the importance of "an explanation for the survival value of learning and ... an investigation of the innate information contained in the teaching mechanisms achieving it." For Lorenz, as we have seen, "innate information" is contained in the "genetic blueprint" to which Schwartz refers.

The existence of adaptive specializations of learning ability is an important problem for the psychology of learning, and one that is, belatedly, starting to receive the attention that it merits (for recent reviews, see Domjan and Galef, 1983; Johnston, 1981; Johnston & Pietrewicz, 1985; Shettleworth, 1983). However, to assume that these specialized capabilities are "innately given," are supplied by a "genetic blueprint," or represent "inherent predispositions" of the animal is simply to replace the empirical error of assuming the generality of learning mechanisms with the more serious conceptual one of assuming that one can usefully speak of their specialization as being "innate." Constraints on learning, like other characteristics of an animal, have a developmental history, and it remains an important question to determine what animal-environment interactions underlie their development. Domjan and Galef (1983, p. 153) make this point when they caution that "available evidence does not permit the conclusion that frequently discussed examples of biological constraints on learning are any more independent of past

⁸ From *The Psychology of Learning and Behavior* (2nd ed., p. 511) by B. Schwartz, 1984, New York: Norton. Copyright 1984 by W. W. Norton & Co., Inc. Reprinted by permission.

experience than many traditional limitations on learning" (such as prior experience with the stimuli involved in a conditioning experiment, for example).

The existence of "innate specializations" of learning capacity has been proposed by students of human learning as well, one of the best-known proposals being Chomsky's (1968, 1978) "language acquisition device" (see L. R. Gleitman, 1984). Chomsky (1957) argued that the characteristics of human language learning make it vanishingly unlikely that the general principles of psychological learning theory can account for the way in which language is learned. He proposed that some aspects of linguistic structure (the "universal grammar") "are available to the language learner without relevant experience [and so it is] only rational to suppose that these mechanisms are genetically determined" (Chomsky, 1978, p. 214-215). Chomsky's reservations about the adequacy of traditional learning theory to account for language are doubtless well-founded, but his willingness to accept genetically determined aspects of language structure as the alternative is unfortunate. Whatever capabilities the human infant brings to the linguistic environment have a developmental history, and understanding language involves the analysis of that history. Passing the buck for a developmental explanation of language to genetics does not help.

Hard-Wired Versus Soft-Wired Behavior

The last modern version of the old learned-innate dichotomy to be discussed appeals specifically to the neural structures that underlie the behavior in question. Hard-wired behavior is developmentally inflexible, specialized in its function, and depends on neural structures whose organization is specified by the genes. Soft-wired behavior is readily modifiable in development, more adaptable in function, and depends on experience provided by the environment. The metaphor is grounded in a distinction in computer science between those capabilities of a computer that depend on the physical structure of the hardware, and those that depend on the way that hardware is instructed by programs. In the neurobiological literature, the distinction was made especially clearly by Jacobson (1974), who identified two classes of neurons, corresponding to the hard-wired and soft-wired structure of the brain, respectively. The structure and function of Class I neurons are rigidly specified by the genes, and are hence determined by the evolutionary history of the species; on the other hand, the structure and function of Class II neurons are under less strict genetic control and depend on the experience and sensory input available to the individual. Thus Jacobson is maintaining, albeit at the neural rather than the behavioral level of analysis, the same distinction between genetically determined and experientially determined aspects of the phenotype as that found in Lorenz's writings. Interestingly enough, Jacobson maintains this distinction in a section of his paper in which he also emphasizes the importance of the interactionist perspective on development: "The obligatory interaction between the organism and its environment, and therefore, the interdependence of nature and nurture, is a well-known theme" (Jacobson, 1974, p. 162). This juxtaposition illustrates the difficulty that many writers have in seeing the fundamental incompatibility between the interactionist view of development and the attribution of separate aspects of the phenotype to the genes and to the environment.

A rather similar perspective is expressed by Hubel and Wiesel (1977), reviewing their seminal work on the functional organization of the striate visual cortex (area 17):

In addressing the problem of the development of area 17 [in the monkey], it seemed to us that the first question to ask was whether the system as we know it in the adult, with its hierarchy of cells, its topographic map and its intricate architecture, is all present at birth *and thus presumably determined genetically* [italics added], or whether some or all of the specificity depends on the details of postnatal experience. Our previous work in cats ... had led us to conclude that in that species genetics was the main, if not the sole determinant in the formation of area 17, but the problem was complicated by the immaturity of the cat's visual system at birth and a difficulty in knowing whether binocular deprivation effects were a result of holding back postnatal maturation or of withholding specific experience. (pp. 43-44)⁹

The first sentence of this passage illustrates the confusion that arises when the term "innate" is used to refer to whatever characteristics are present at birth (i.e., as a synonym for "congenital"). The false inference is then drawn that one can speak of congenital characteristics as being genetically determined. Of course, the question of how much of the adult cortical organization depends on visual experience obtained after birth is perfectly well-formulated and in itself implies no false dichotomies. It is only when the only other source of cortical organization is considered to be "genetic determination" that problems arise. The second sentence, with its distinction between holding back maturation and withholding specific experience, echoes clearly Lorenz's distinction between "bad rearing" and a deprivation experiment. While the metaphor of "hardwiring" as a way of referring to whatever is present at birth (what "comes from the factory," so to speak) is unobjectionable, though not especially illuminating, the extension of the metaphor to imply genetic determination is thoroughly misleading. Unfortunately, the extension almost invariably follows from the use of the term.

ELEMENTS OF THE INTERACTIONIST APPROACH TO BEHAVIORAL DEVELOPMENT

The prevalence of dichotomous thinking in development will not be reduced until workers in the area become comfortable with the alternative provided by the interactionist approach. A clear statement of this approach was made 60 years ago by Carmichael (1925), and it has been restated and elaborated in a number of subsequent publications (e.g., Gottlieb, 1976; Hofer, 1981; Kuo, 1976; Lehrman, 1953, 1956, 1970; Schneirla, 1956, 1966). In the preceding discussion I have pointed out the major objections to dichotomous thinking in development, in both its classical and its more recent versions. In the remainder of this paper I shall discuss the alternative, interactionist perspective, focusing on those aspects of the approach that seem to have been most widely misunderstood, and that may have contributed the most to its rather limited assimilation in the behavioral literature.

Obvious and Nonobvious Experiential Influences on Behavioral Development

One of Lehrman's (1953) original criticisms of the deprivation experiment as a means of analyzing behavioral development was that it addresses only the most obvious experiential influences on development— those that are provided, for example, by opportunities for conditioning, observation, imitation, and sensory preexposure. But the animal-environment interaction that produces development involves many more components than just these, and the goal of the interactionist approach to developmental analysis is to identify all of the

⁹ From "Functional architecture of macaque monkey visual cortex" (pp 43-44) by D. H. Hubel and T. N. Wiesel (Proceedings of the Royal Society of London, B, 198, 1-59). Copyright 1977 by The Royal Society of London. Reprinted by permission.

experiential contributions to development, not just the most obvious ones (Schneirla, 1956). Important contributions may be made to development by aspects of the animal's experience that are not at all obviously related to the behavior whose development they support. For example, Gottlieb (1978) has shown that in the mallard duckling (*Anas platyrhynchos*) prenatal auditory experience with the *embryonic* calls of either self or siblings is essential to the development of a highly specific postnatal preference for the *maternal* call of the duckling's own species. (A similar dependency on the calls of siblings during the early posthatching period has been found in the wood duckling, *Aix sponsa*; Gottlieb, 1980). In this example of development, the requisite experience (embryonic stimulation) is quite different from the later behavior (specific preference for the maternal call) whose development it supports. In evaluating such results, the temptation is to ask (incredulously): "But what on earth could the duckling learn from hearing its own embryonic call about the characteristics of the maternal call?" The answer, of course, is "Nothing," but the question misses the point of the example, which was to demonstrate that not all cases in which experience contributes to the development of behavior involve the obvious kinds of contribution that are implied by the word "learning." The interactionist approach does not claim that all behavior is learned, but rather that all behavior results from an interaction between the animal and its environment. The aim of its analysis is to unpack that interaction, some of whose elements may be less obvious than others (Gottlieb, 1980, 1981).

The importance of nonobvious experiential contributions to development is sometimes underestimated because of the apparent improbability that they could "convey information" to the developing animal. For example, Kuo (1932) suggested that the passive movements of an embryonic chick's head, caused by the beating of its heart, might be important precursors of the later development of pecking movements aimed at food. Lorenz (1965) ridiculed this suggestion by asking how the chick could possibly learn anything about the adaptive necessity for making pecking movements while it was still in the egg. Clearly it cannot, and so Lorenz concluded that prenatal head movements could not carry any information relevant to the development of postnatal pecking. As we have seen, however, the only way to determine whether some event carries information for the developing organism is to alter the event and see if the course of development is affected. (No evidence has ever been presented to either support or refute Kuo's suggestion.) Our intuitions about which events are likely to carry information may be a useful source of hypotheses on which to base experiments, but they should not be allowed (as Lorenz allows his) to replace empirical analyses of the developing system. The fact that it is not obvious *to us* why some developmental event might be necessary to enable subsequent development to follow its normal course reflects only our limited understanding of the determinants of behavioral development. The distinction between obvious and nonobvious experiential contributions to development rests on our subjective impression of what makes *prima facie* sense in development. It is critically important that we do not allow such judgments to inhibit our investigations of what is in fact important in the development of behavior.

As the less obvious experiential influences on development are further analyzed, it will become easier to frame plausible hypotheses about the possible role of such influences in other systems. For example, Gottlieb's (1978) demonstration of the importance of prenatal self-stimulation for auditory development in the mallard duckling suggests that the role of self-stimulation in song

development among passerine birds might bear investigating. Perhaps some of the aspects of song development in the swamp sparrow and song sparrow that do not appear to depend on exposure to song after hatching (Marler & Sherman, 1983) do depend on auditory stimulation provided by the young bird itself, for example by its begging calls. That possibility was raised by Nottebohm (1972) but it has never received experimental attention, or even serious consideration, by investigators of bird song development. (Marler & Sherman, 1983, p. 529, allude to the possibility in passing, but dismiss it in a phrase.) Like all other aspects of behavioral development, the development of bird song depends on a complex of epigenetic interactions within the developing animal-environment system, interactions that may involve both obvious and nonobvious contributions by the environment.

Invariant Outcomes of Behavioral Development

The persistence of a dichotomous approach to behavioral development seems to have been buttressed by a concern with explaining the fact that at least some aspects of the behavioral phenotype show remarkable invariance from one individual to another, although others may be quite variable. Typically, invariance in development is attributed to genetic determination, variability to the effects of the environment. Thus the facts that all normal human infants will suck on a nipple immediately after birth, that all children learn to speak a language, and that smiling is a virtually universal human social signal are all taken to indicate the importance of the genes in determining at least some outcomes of behavioral development. All human beings share a common genetic heritage by virtue of belonging to the human species, and it is that commonality that explains the existence of behavioral similarities. Lumsden and Wilson (1981) carry such reasoning to its extreme when they attribute *all* regularities in development to the influence of the genes. The assumption underlying such reasoning seems to be that since environments are inherently variable and unstable, environmental influences cannot be invoked to account for the existence of behavioral invariances in development (L. R. Gleitman, 1984, p. 555). Given the enormous range of conditions under which human beings develop (so this argument goes), how can it be that we all smile to indicate friendliness (Eibl-Eibesfeldt, 1979) unless the genes determine the development of that social signal? The apparent plausibility of this assumption rests on two misunderstandings. First, that any environmental influence on development must be of the kind normally described as learning (see above); and second, that the environment cannot provide invariant sources of information for development.

The first of these misunderstandings has already been dealt with at some length. The interactionist view does not argue that the development of smiling more or less universally across human cultures must depend on there being identical opportunities for learning. It argues that such development must depend on an organism-environment interaction in which other, less obvious kinds of experience may play a role. The second misunderstanding is related to the first, because the kinds of environmental influences that are necessary for learning are often quite variable, in which case they would not be capable of ensuring invariant developmental outcomes. But there are many other environmental influences that are in fact quite invariant, some universally, others less so, but still sufficiently. For example, the self-stimulation that Gottlieb (1981) showed to be essential for the normal development of a duckling's response to its mother's call is absolutely invariant over the prenatal environments of all mallard ducklings. All ducklings vocalize in the egg, and so this source of environmental influence on development is always available to ensure an invariant developmental outcome. Prenatal influences of this type may be

quite common in mammalian development, where the uterus provides a highly buffered environment in which development can proceed along an invariant trajectory, while being, at the same time, sensitive to many (invariant) environmental influences. Other invariant aspects of the environment that have been shown to influence the development of one or more species include the force and direction of gravity (Dennison & Shropshire, 1984), and the rotation of stars in the night sky (Emlen, 1975). An invariant outcome in behavioral development can readily be attained on the basis of an interaction with some aspect of the environment, just so long as that aspect of the environment is itself invariant across the range of situations in which development takes place (Johnston, 1981:: Lehrman, 1970; Petrunkevich, 1924). The explanation of developmental invariance does not require that we invoke the genetic determination of behavior.

Psychobiological Continuity and Behavioral Development

The originators of the interactionist approach (e.g., Carmichael, 1925; Lehrman, 1953; see Oppenheim, 1982) were psychobiologists whose interests spanned the behavior, physiology, and anatomy of the developing animal. For the psychologist interested primarily in the behavior or cognitive abilities of the individual, the interactionist approach sometimes seems to lack a compelling account for the development of those abilities that cannot be explained as the outcome of learning. If the ability of neonates to make phonemic contrasts is not learned (and let us suppose it is not), then how does it arise? Proponents of the dichotomous approach to development have a ready answer, namely that the genes specify that aspect of human behavioral development. If the details of such an account are lacking, psychologists often assume that to be because we lack a detailed understanding of genetic function, not because of any inadequacy inherent in the account itself. Because the genes are so mysterious, it is easy to attribute organizational properties to them sufficient to solve any developmental problem that cannot be explained in terms of learning. The interactionist approach replaces the mysterious, but somehow reassuring, power of the genes with a series of unanswered questions about the prenatal origins of the neural and other structures underlying speech perception and production, questions whose answers require considerable information about the anatomy and physiology of the developing embryonic nervous system. Even where the necessary information is available (and most often it is not), most psychologists are simply not interested in such a detailed excursion into experimental embryology. Resisting, quite legitimately, the apparent implication of the interactionist approach that they become developmental physiologists, it is not surprising that many psychologists prefer to adopt a dichotomous account of development.

How, then, can psychologists who are not primarily (or even slightly;) interested in the physiology of the developing organism talk about the unlearned capabilities of their subjects without succumbing to the temptation to attribute magical powers to the genes? Most straightforwardly, by simply recognizing that at any point in its life, the individual already has a developmental history that can quite legitimately be assumed as a starting point for explanations of subsequent development. A theory of postnatal language development, for example, can build on the linguistic abilities of the newborn and leave the explanation of those abilities to a possibly quite different theory of prenatal language development. It is important, however, to appreciate that those neonatal abilities are not explained by attributing them to the genes—there is a developmental explanation to be given, even though the psychologist who is interested in postnatal language development may not be interested in doing so. But one who is interested in

seeking that developmental explanation is likely to find the interactionist approach of far greater assistance than a dichotomous approach that merely invokes "the genes" as causal determinants of linguistic ability, without any suggestion as to how the genes perform that feat. Attributing the capabilities of the newborn infant to a history of prenatal developmental interactions between the embryonic nervous system and its environment does not explain their origin, but it does usefully indicate where such an explanation will be found in a way that attributing them to the genes does not.

Of course, as we pursue the antecedents of behavior further and further back into embryonic life, we find the explanatory power of psychological constructs of less and less relevance to the very rudimentary psychological abilities of the embryo, and biological constructs become progressively more important. One of the greatest challenges for developmental psychobiology is to find explanations that can encompass the transformation from the purely biological status of the very early embryo to the manifestly psychological status of the newborn (Hofer, 1981). The psychobiological continuity inherent in the interactionist account of development gives it great potential as a source of such explanations.

On Genes and Interactions in Development

Before concluding, a few words should be said about the use and misuse of the term "interaction" in developmental analysis and about some of the confusion that has arisen over how the interactionist position treats genetic contributions to behavioral development. Because the interactionist approach proceeds conceptually by refusing to partition the phenotype between genetic and environmental determinants, and empirically by analyzing the interaction between the animal and the environment, it sometimes appears to ignore the genes altogether. Those who espouse an interactionist approach to development are often accused of being radical environmentalists, denying that the genes play any significant role at all in development. For example, Mueller (1983, p. 183) criticized Lehrman's position on just those grounds and urged that "a better way [to conceptualize development] must be found." The problem is that Lehrman's position (and the interactionist position generally) is often viewed as involving an interaction between genes and the environment, whereas it actually involves an interaction between the *phenotype* and the environment. If one supposes that the genes and the environment interact directly to produce the phenotype, then any analysis that fails to explicitly mention one member of the interaction will inevitably be seen as favoring the other. But an organism's genes do not interact with its environment in the course of development; the developing phenotype interacts with the environment and the details of this interaction provide the focus of the experimental analysis of development from the interactionist perspective. Of course, the genes do contribute, doubtless in many important ways, to behavioral development. However, the exact form of this contribution is, for the most part, quite unclear, and techniques that might be used in its analysis have not yet been applied to the complex forms of behavior of greatest interest to psychologists and ethologists.¹⁰ Thus students of behavioral development have generally been

¹⁰ A discussion of these techniques would lie far outside the scope of this paper, but Stent (1981) provides a lucid and highly readable account that is accessible to the nonspecialist. One technique that seems of particular promise is that of forming genetic chimeras in mice. If the morulas (very early embryos) of two mice, one genetically normal, the other carrying a mutant gene known to affect behavior, are dissociated in solution and the cells allowed to recombine, they will form an embryo some of whose cells are of normal genotype while others are mutant. When the mouse develops, it may show the mutant behavioral phenotype, in which case cells in those tissues that are involved in the development of that phenotype must be of mutant genotype. By using histological techniques that

forced, by empirical and technical necessity, to focus their attention on the animal-environment interaction, as the only aspect of the problem open to analysis.

The idea that an interactionist approach to development means studying gene-environment interactions has been given strong but spurious support by an unfortunate terminological coincidence. The term "interaction" is also used in population genetics, but with a very different meaning. Population geneticists are concerned with the analysis of phenotypic variation in populations, not phenotypic development in individuals. They have devised statistical techniques that allow that variation to be partitioned among genetic variation, environmental variation, and the interaction between the two. But accounting for *variation* in a trait among individuals in a population is quite a different matter from accounting for its *development* in the individuals that make up that population. The analysis of variation in population genetics answers the question "Why do the phenotypes of individuals in this population differ from one another?" Such variation may arise in part because individuals differ genetically, in part because they develop in different environments, and in part because different genotypes respond differently to environmental variation (the "genotype x environment interaction" term in the analysis of variation). The analysis of development answers the question "How does the phenotype of an individual in this population come to be the way that it is?" As argued in this paper, phenotypes arise from an interaction between the developing animal and its environment. The two uses of the term "interaction" in these different endeavors have no more in common than do the two uses of the term "significant" in statistics and in literary criticism. Both Lehrman (1970) and Lewontin (1974) have very clearly explicated the difference between the analysis of variation (in population genetics) and the analysis of causes (in development). The coincidence of the term "interaction" in both analyses sometimes makes it difficult for critics of dichotomous thinking in development to be taken seriously. Their targets can too easily evade the issue by pointing approvingly to the analysis of interactions in population genetics, even though that analysis has nothing to do with the developmental issue on which they are being criticized.

CONCLUSION

Despite frequent protestations to the contrary, the use of conceptual dichotomies to think about behavioral development remains as pervasive today as it has ever been. The terms in which those dichotomies are expressed have changed, but they are no more adequate to the task of resolving the problems of development than was the distinction between learned and innate behavior from which they ultimately derive. Of course, there can be no objection to categorizing the phenomena of behavioral development as a basis for future explanation. It is clear that some behavior patterns are highly resistant to experiential modification and others are less so; that some patterns are present at birth and others are not; that some patterns depend on practice for their normal development whereas others require less obvious kinds of experience. What needs to be resisted is the temptation to see these classifications as implying different kinds of explanation for

reveal biochemical markers associated only with the mutant genotype, the relevant tissues can be identified, enabling the site of action of the mutant gene to be specified. Many such experiments must be performed to identify the site and time of action of such genes with any precision, and their results cannot be given a clear developmental interpretation without detailed information about the precise genetic effect of the mutation being used (whether it produces an abnormal gene product, or no product at all, for example). Nonetheless, this technique, and others like it, offer some idea of how the role of gene action in behavioral development might in principle be studied, while at the same time indicating the tremendous technical obstacles that will lie along the way.

development. Although they may be valuable guides to our thinking, they only help in specifying the problems of development that need solving. Pointing out that a pattern of behavior is present at birth does not explain *how* it comes to be present at birth—the problem of development needs to be solved for congenital as well as other patterns of behavior (e.g., Gottlieb, 1981). None of these points is new. They have all been made before, by Weismann (1894), Carmichael (1925), Lehrman (1953, 1970), Gottlieb (1976), and others, but for some reason the dichotomies persist. There is a powerful attraction in the attempt to assign, under some set of labels, different aspects of the phenotype to the genes and to experience, to what is biologically given and what is psychologically acquired. That approach has become so much a part of our thinking about development that it frequently goes unrecognized by those who adopt it. The myth prevails that by abandoning just the terms "innate" and "learned" we can avoid the dangers of dichotomous thinking, and those who continue to criticize the dichotomies often end up being accused of beating a dead horse. But this is one dead horse that continues to demonstrate impressive vitality and remarkable staying power.

REFERENCES

- Bootzin, R. R., Loftus, E. R., & Zajonc, R. B. (1983). *Psychology today* (5th ed.). New York: Random House.
- Carmichael, L. (1925). Heredity and environment: Are they antithetical? *Journal of Abnormal and Social Psychology*, 20, 245-260.
- Chomsky, N. (1957). Review of B. R Skinner's *Verbal behavior*. *Language*, 35, 26-58. Chomsky, N. (1968). *Language and mind*. New York: Harcourt, Brace.
- Chomsky, N. (1978). On the biological basis of language capacities. In G. A. Miller & E. Lenneberg (Eds.), *Psychology and biology of language and thought* (pp. 199-220). New York: Academic Press.
- Dennison, D. S., & Shropshire, W., Jr. (1984). The gravireceptor of *Phycomyces*: Its development following gravity exposure. *Journal of General Physiology*, 84, 845-859.
- Diamond, S. (1971). Gestation of the instinct concept. *Journal of the History of the Behavioral Sciences*, 7, 323-336.
- Diamond, S. (1974). Four hundred years of instinct controversy. *Behavior Genetics*, 4, 237-252.
- Domjan, M., & Galef, B. G., Jr. (1983). Biological constraints on instrumental and classical conditioning: Retrospect and prospect. *Animal Learning and Behavior*, 11, 151-161.
- Eibl-Eibesfeldt, I. (1956). Über der Ontogenetische Entwicklung der Technik des Nüsseöffnens vom Eichhornchen (*Sciurus vulgaris*). *Zeitschrift für Säugetierkunde*, 21, 132-134.
- Eibl-Eibesfeldt, I. (1961). The interactions of unlearned behavior patterns and learning in mammals. In J. E. Delafresnaye (Ed.), *Brain mechanisms and learning* (pp. 53-73). Oxford: Blackwell.

Eibl-Eibesfeldt, I. (1979). Human ethology: Concepts and implications for the sciences of man. *Behavioral and Brain Sciences*, 2, 1-57.

Eimas, P. D. (1985). The perception of speech in early infancy. *Scientific American*, 252(1), 46-52.

Ekman, P., Levenson, R., & Friesen, W. V. (1983). Autonomic nervous system activity distinguishes among emotions. *Science*, 221, 1208-1210.

Emlen, S. T. (1975). The stellar-orientation system of a migratory bird. *Scientific American*, 223(2), 102-111.

Engle, G. N., Rothstein, S. I., Osenberg, C. W., & McGinley, M. A. (1984). Signals of status in wintering white-crowned sparrows, *Zonotrichia gambelii*. *Animal Behaviour*, 32, 86-93.

Garcia, J., & Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science*, 4, 123-124.

Gleitman, H. (1981). *Psychology*. New York: Norton.

Gleitman, L. R. (1984). Biological predispositions to learn language. In P. Marler & H. S. Terrace (Eds.), *The biology of learning* (pp. 553-584). Berlin: Springer-Verlag.

Gottlieb, G. (1976). The roles of experience in the development of behavior and the nervous system. In G. Gottlieb (Ed.), *Neural and behavioral specificity* (pp. 1-25). New York: Academic Press.

Gottlieb, G. (1978). Development of species identification in ducklings: IV. Change in species-specific perception caused by auditory deprivation. *Journal of Comparative and Physiological Psychology*, 92, 375-387.

Gottlieb, G. (1980). Development of species identification in ducklings: VII. Highly specific early experience fosters species-specific perception in wood ducklings. *Journal of Comparative and Physiological Psychology*, 94, 1019-1027.

Gottlieb, G. (1981). Roles of early experience in species-specific perceptual development. In R. N. Aslin, J. R. Alberts, & M. P. Petersen (Eds.), *Development of perception* (Vol pp. 5-44). New York: Academic Press.

Grant, B. R. (1984). The significance of song variation in a population of Darwin's finches. *Behaviour*, 89, 90-106.

Grohmann, J. (1939). Modification oder Funktionsreife? *Zeitschrift für Tierpsychologie*, 132-144.

- Haig, K. A., Rawlins, J. N. P., Olton, D. S., Mead, A., & Taylor, B. (1983). Food searching strategies of rats: Variables affecting the relative strength of stay and shift strategies. *Journal of Experimental Psychology: Animal Behavior Processes*, 9, 337-348.
- Hinde, R. A. (1955). The modifiability of instinctive behavior. *Advances in Science*, 12, 19-24.
- Hofer, M. A. (1981). *The roots of human behavior*. San Francisco: Freeman.
- Hubei, D. H., & Wiesel, T. N. (1977). Functional architecture of macaque monkey visual cortex. *Proceedings of the Royal Society of London, B*, 198, 1-59.
- Jacobson, M. (1974). A plenitude of neurons. In G. Gottlieb (Ed.), *Aspects of neurogenesis* (pp. 151-166). New York: Academic Press.
- Jensen, D. D. (1961). Operationism and the question "Is this behavior learned or innate?" *Behaviour*, 17, 1-8.
- Johnston, T. D. (1981). Contrasting approaches to a theory of learning. *Behavioral and Brain Sciences*, 4, 125-173.
- Johnston, T. D. (1982). Learning and the evolution of developmental systems. In H. C. Plotkin (Ed.), *Learning, development, and culture* (pp. 411-442). Chichester: Wiley.
- Johnston, T. D., & Pietrewicz, A. T. (Eds.). (1985). *Issues in the ecological study of learning*. Hillsdale, NJ: Erlbaum.
- King, A. P., & West, M. J. (1983). Female perception of cowbird song: A closed developmental program. *Developmental Psychobiology*, 16, 335-342.
- King, A. P., & West, M. J. (1987). Different outcomes of synergy between song production and song perception in the same subspecies (*Molothrus ater ater*). *Developmental Psychobiology*, 20, 177-187.
- Konishi, M. (1965). The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Zeitschrift für Tierpsychologie*, 22, 771-783.
- Kroodsma, D. E. (1984). Songs of the alder flycatcher (*Empidonax alnorum*) and willow flycatcher (*Empidonax traillii*) are innate. *Auk*, 101, 13-24.
- Kroodsma, D. E., & Pickert, R. (1984). Repertoire size, auditory templates, and selective vocal learning in songbirds. *Animal Behaviour*, 32, 395-399.
- Kuo, Z.-Y. (1921). Giving up instincts in psychology. *Journal of Philosophy*, 18, 645-664.
- Kuo, Z.-Y. (1932). Ontogeny of embryonic behavior in Ayes: IV. The influence of embryonic movements upon the behavior after hatching. *Journal of Comparative Psychology*,

14, 109-122.

Kuo, Z.-Y. (1976). *The dynamics of behavior development* (enlarged ed.). New York: Random House.

Lehrman, D. S. (1953). A critique of Konrad Lorenz's theory of instinctive behavior. *Quarterly Review of Biology*, 28, 337-363.

Lehrman, D. S. (1956). On the organization of maternal behavior and the problem of instinct. In P.-P. Grasse (Ed.), *L'Instinct dans le comportement des animaux et de l'homme* (pp. 475-520). Paris: Masson.

Lehrman, D. S. (1970). Semantic and conceptual issues in the nature-nurture problem. In L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.), *Development and evolution of behavior* (pp. 17-50). San Francisco: Freeman.

Lewontin, R. C. (1974). The analysis of variance and the analysis of causes. *American Journal of Human Genetics*, 26, 400-411.

Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels. *Journal für Ornithologie*, 83, 137-213, 289-413.

Lorenz, K. (1937a). The companion in the bird's world. *Auk*, 54, 245-273.

Lorenz, K. (1937b). Über die Bildung des Instinkt-begriffes. *Naturwissenschaften*, 25, 289-300, 307-318, 324-331.

Lorenz, K. (1956). The objectivistic theory of instinct. In P.-P. Grasse (Ed.), *L'Instinct dans le comportement des animaux et de l'homme* (pp. 51-76). Paris: Masson.

Lorenz, K. (1957a). Companionship in bird life. In C. H. Schiller (Ed.), *Instinctive behavior* (pp. 83-128). New York: International Univ. Press.

Lorenz, K. (1957b). The nature of instinct. In C. H. Schiller (Ed.), *Instinctive behavior* (pp. 129-175). New York: International Univ. Press.

Lorenz, K. (1965). *Evolution and modification of behavior*. Chicago, IL: Univ. of Chicago Press.

Lorenz, K. (1970). The establishment of the instinct concept (R. Martin, Trans.). In K. Lorenz, *Studies in animal and human behavior* (pp. 259-315). Cambridge, MA: Harvard Univ. Press.

Lorenz, K., & Tinbergen, N. (1938). Taxis and Instinkt-handlung in der Eirollbewegung der Graugans I. *Zeitschrift für Tierpsychologie*, 2, 1-29.

Lumsden, C. J., & Wilson, E. O. (1981). *Genes, mind and culture: The coevolutionary process*. Cambridge, MA: Harvard Univ. Press.

- Mailer, P. (1970). A comparative approach to vocal learning: Song development in white-crowned sparrows. *Journal of Comparative and Physiological Psychology Monographs*, 71(No. 2, Pt. 2), 1-25.
- Mailer, P. (1976). Sensory templates in species-specific behavior. In J. C. Fentress (Ed.), *Simpler networks and behavior* (pp. 314-329). Sunderland, MA: Sinauer Assoc.
- Mailer, P., & Sherman, V. (1983). Song structure without auditory feedback: Emendations of the auditory template hypothesis. *Journal of Neuroscience*, 3, 517-531.
- Mayr, E. (1974). Behavior programs and evolutionary strategies. *American Scientist*, 62, 650-659.
- Moltz, H. (1984). Why rat young respond to the maternal pheromone. In G. Greenberg & E. Tobach (Eds.), *Behavioral evolution and integrative levels* (pp. 277-288). Hillsdale, NJ: Erlbaum.
- Mueller, H. C. (1983). What will we gain from an ecological approach to learning? Another ethologist's view. *Behavioral and Brain Sciences*, 6, 182-183.
- Nash, J. (1978). *Developmental psychology: A psychobiological approach* (2nd ed.). Englewood Cliffs, NJ: Prentice-Hall.
- Nottebohm, F. (1972). Neural lateralization of vocal control in a passerine bird. II. Subsong, calls and a theory of vocal learning. *Journal of Experimental Zoology*, 179, 35-49.
- Olton, D. S., & Schlosberg, P. (1978). Food searching strategies of young rats: Win-shift predominates over win-stay. *Journal of Comparative and Physiological Psychology*, 92, 609-618.
- Oppenheim, R. W. (1982). Preformation and epigenesis in the origins of the nervous system and behavior: Issues, concepts, and their history. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Perspectives in ethology, Vol5: Ontogeny* (pp. 1-100). New York: Plenum.
- Oyama, S. (1982). A reformulation of the idea of maturation. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Perspectives in ethology, Vol5: Ontogeny* (pp. 101-131). New York: Plenum.
- Oyama, S. (1985). *The ontogeny of information: Developmental systems and evolution*. Cambridge: Cambridge Univ. Press.
- Papalia, D. E., & Olds, S. W. (1985). *Psychology*. New York: McGraw-Hill.
- Petrinovich, L. (1985). Factors influencing song development in the white-crowned sparrow. (*Zonotrichia leucophrys*). *Journal of Comparative Psychology*, 99, 15-29.

Petrunkevich, A. (1924). Environment as a stabilizing factor. In M. R. Thorpe (Ed.), *Organic adaptation to environment* (pp. 67-110). New Haven, CT: Yale Univ. Press.

Rowley, I., & Chapman, G. (1986). Cross-fostering, imprinting, and learning in two sympatric species of cockatoo. *Behaviour*, 96, 1-16.

Schneirla, T. C. (1956). Interrelationships of the "innate" and the "acquired" in instinctive behavior. In P.-P. Grasse (Ed.), *L'Instinct dans le comportement des animaux et de l'homme* (pp. 387-452). Paris: Masson.

Schneirla, T. C. (1966). Behavioral development and comparative psychology. *Quarterly Review of Biology*, 41, 283-302.

Schwartz, B. (1984). *Psychology of learning and behavior* (2nd ed.). New York: Norton.

Seyfarth, R. B., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour*, 28, 1070-1094.

Shannon, C. E., & Weaver, W. (1949). *The mathematical theory of communication*. Urbana, IL: Univ. of Illinois Press.

Shettleworth, S. J. (1972). Constraints on learning. In D. S. Lehrman, R. A. Hinde, & E. Shaw (Eds.), *Advances in the study of behavior* (Vol. 4, pp. 1-72). New York: Academic Press.

Shettleworth, S. J. (1982). Function and mechanism in learning. In M. Zeiler & P. H. Harzem (Eds.), *Advances in analysis of behavior* (Vol. 3, pp. 1-39). New York: Wiley.

Stent, G. (1981). Strength and weakness of the genetic approach to the development of the nervous system. In W. M. Cowan (Ed.), *Studies in developmental neurobiology* (p. 288-321). New York: Oxford Univ. Press.

Tinbergen, N. (1951). *The study of instinct*. Oxford: Oxford Univ. Press.

Weismann, A. (1894). *The effect of external influences upon development* (The Romanes Lecture). London: Henry Frowde.

West, M. J., King, A. P., & Eastzer, D. H. (1981). The cowbird: Reflections on development from an unlikely source. *American Scientist*, 69, 57-66.

Wiener, N. (1948). *Cybernetics*. New York: Wiley.

Zimbardo, P. G. (1985). *Psychology and life* (11th ed.) Glenview, IL: Scott, Foresman.