



Innateness and the instinct to learn

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ABSTRACT

Concepts of innateness were at the heart of Darwin's approach to behavior and central to the ethological theorizing of Lorenz and, at least to start with, of Tinbergen. Then Tinbergen did an about face, and for some twenty years the term 'innate' became highly suspect. He attributed the change to Lehrman's famous 1953 critique in which he asserted that classifying behaviors as innate tells us nothing about how they develop. Although Lehrman made many valid points, I will argue that this exchange also led to profound misunderstandings that were ultimately damaging to progress in research on the development of behavior. The concept of 'instincts to learn', receiving renewed support from current theorizing among geneticists about phenotypic plasticity, provides a potential resolution of some of the controversies that Lehrman created. Bioacoustical studies, particularly on song learning in birds, serve both to confirm some of Lehrman's anxieties about the term 'innate', but also to make a case that he threw out the genetic baby with the bathwater. The breathtaking progress in molecular and developmental genetics has prepared the way for a fuller understanding of the complexities underlying even the simplest notions of innate behavior, necessary before we can begin to comprehend the ontogeny of behavior.

Key words: innateness, song learning, phenotypic plasticity, behavioral genetics, Tinbergen's four questions.

INTRODUCTION

One of the great issues that have long confronted biologists, philosophers, and social scientists is the controversy about nature and nurture. To what extent are we products of our genetic make-up, and to what extent are we reflections of the cumulative consequences of the myriad of experiences over a lifetime? In our own case this is a conundrum that we will never solve, but with animals we may have some chance of gaining at least a rough understanding of the principles involved. It has been a central issue in the study of animal behavior for a long time, especially in that aspect of bioacoustics with which

I have been most intimately involved, vocal communication in birds, and the development of birdsong.

HISTORICAL BACKGROUND

I was lucky, as a student, to be present at the very beginning of birdsong studies, and to participate in the initial spread of ethology, first in Europe, and then in America. These were exciting times in the early 1950s, when so much about the study of behavior was in a state of ferment, much of it triggered by the contributions of Konrad Lorenz (Fig. 1).

Many new directions were emerging, summarized in Tinbergen's list of issues to be addressed, outlined by him for me as external examiner on my PhD thesis committee. Interestingly he was

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not alone in trying to forecast the future. Julian Huxley, acknowledged as an influential colleague by Lorenz, (Fig. 1) wrote an appreciative piece called ‘Lorenzian ethology’, with a list similar to Tinbergen’s (Huxley 1963). The two of them shared the same three main points of focus: (1) the causation of behavior, by which they meant the underlying physiological machinery; (2) the survival value of behavior; and (3) its role in evolution. In the years that followed, there has been dramatic progress in all three of these areas, and research in bioacoustics has made major contributions in all of them ranging from insects (e.g. Otte 1977, Michelsen and Larsen 1983, Michelsen 1992, Bennet-Clark 1989, 1998, 1999) to anurans (e.g. Ryan 1985, Wilczynski and Ryan 1999, Schwartz 2001, Gerhardt and Huber 2002), birds (Thorpe 1961, Kroodsma and Miller 1982, 1996, Catchpole and Slater 1995) and mammals (Eisenberg 1976, Gould 1983, Cheney and Seyfarth 1990). But Tinbergen chose to add a fourth area, the development of behavior (Tinbergen 1963), which was destined to become something of an orphan. Even today we have no comprehensive theory of behavioral ontogeny. I have spent much time trying to understand why it happened that progress in the study of development was the slowest of the four areas of study. In doing so, I have gone back repeatedly to other events taking place in the behavioral sciences in the fifties, many of them directly provoked by the renewed interest in instinctive behavior. That is the theme that I want to present here.

THE CONCEPT OF INNATENESS

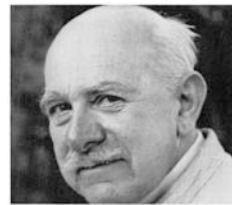
Lorenz, Tinbergen, and my own teacher and mentor, W.H. Thorpe, like Darwin, were all fully convinced of the value of the concept of instinct, defined by Webster’s dictionary as “an in-born tendency to behave in a way characteristic of a species”. As a medical student in Vienna, Lorenz was exposed to the ferment of phylogenetic theorizing in comparative anatomy and morphology, mostly based on the study of bones and skeletons. The young Lorenz was more interested in behavior,



Konrad Lorenz (1903 - 1989)



Nikolaas Tinbergen (1907 - 1988)



Oskar Heinroth (1871 - 1945)



Julian Huxley (1887 - 1975)



Daniel S. Lehrman (1919 - 1972)



Donald O. Hebb (1904 - 1985)

Fig. 1 – Six key figures in the innateness controversy: Lorenz, Tinbergen, Heinroth, Huxley, Lehrman, and Hebb.

but his teachers took the view that behavior was too variable and amorphous to be amenable to the same kind of study. But with the encouragement of his most influential mentor, Oscar Heinroth (Fig. 1), Lorenz became convinced that ethology could be as objective as comparative anatomy. As director of the Berlin Zoo, Heinroth was intimate with the behavior of scores of animals, many of which he raised in captivity, often by hand, especially birds. His monumental ‘Die Vögel Mitteleuropas’, written with his wife, Magdalena Heinroth, is full of details, richly illustrated, about the development of behavior in an

amazing number of birds (Heinroth and Heinroth 1924-1933). Among Lorenz's zoo favorites were waterfowl, and watching them he found that many of the distinctive, species-specific displays they performed in captivity matched those in the wild, even though they had no adult tutors to instruct them. In his 1941 monograph on duck behavior, Lorenz compared in detail 20 species, all of whose displays appeared to him to develop normally in captivity, down to the finest details of nod-swimming and the grunt-whistle and head-up/tail-up, and so on (Lorenz 1941). It seemed natural to regard these displays as instinctive or innate, and the concept of innateness became central to his view of behavior.

Ethologists then began describing how young animals of diverse species, raised under similar conditions, consistently developed distinctive behaviors that were sufficiently stable and stereotyped to yield insights into taxonomy and phylogeny. Lorenz developed his notion of 'fixed action patterns', building on some of Heinroth's ideas, characterizing units of behavior that could be studied in similar terms to anatomical and morphological features.

This in turn was the view embraced by Tinbergen (1951) in his pivotal book on *The Study of Instinct*. It appeared in the year I became a graduate student in Thorpe's laboratory. Tinbergen's commitment to the idea of innate behavior was clear and unequivocal. But over the next few years something strange happened. Tinbergen made a radical change in his position on innateness. His approach to observation and experimentation hardly changed, but his position as a theorist was quite transformed. He joined with others in imposing a virtual taboo on the term 'innate'. The event he held responsible was a 1953 paper by Daniel Lehrman, a leading American animal behaviorist and the world authority on the intricate interactions between hormones and behavior in the reproduction of doves (Fig. 1). He called the paper "A critique of Konrad Lorenz's theory of instinctive behavior". Lehrman's attack on the concept of innateness had a major impact, not only in ethology, but also throughout animal behavior and comparative psychology in general. Subsequently

Tinbergen became much more cautious about using the term 'innate', and he was joined by other leading ethologists, including Patrick Bateson, Robert Hinde, and Gerard Baerends, and many other influential figures. As a consequence, the very foundation on which the ethological approach to the development of behavior was founded suddenly became suspect. In the years that followed, the term 'innate' became a forbidden word. And of course the message was not lost on students who, like me, were in the midst of launching their own careers in animal behavior.

For young and old alike, Lehrman's paper was influential not only because of its cogent criticisms of ethology, but also because of his eloquence, and the tone in which it was written, which was extremely hostile. He almost ridiculed the concept of innateness, stressing the difficulty of excluding environmental influences on ontogeny, especially in the study of behavior. By implication he called into question the very idea that genetical approaches to the study of behavioral development could be of value. Lorenz was furious and, although they became reconciled later, I suspect that he never really forgave Lehrman. At times the confrontation escalated and assumed an almost religious fervor. The aftermath of these angry exchanges could be felt decades later, and I am convinced that the bitterness of the controversy inhibited many in the next generation of behaviorists from even acknowledging the validity of the genetic side of the developmental equation. Years later, Lehrman (1970) was adamant that "the clearest possible genetic evidence that a characteristic of an animal is genetically determined in the sense that it has been arrived at through the operation of natural selection does not settle any questions at all about the developmental processes by which the phenotypic characteristic is achieved during ontogeny", an extreme view, but a view with which, at the time, many others seemed to agree. Thorpe was one of the few who maintained a more balanced viewpoint, and as his student I acquired a degree of skepticism about the whole controversy that I have never entirely lost.

In retrospect, it is my judgment that the Lehrman controversy generated more heat than light. It continued for a remarkably long time. In a symposium on the development and evolution of behavior, published thirteen years after his 1953 bombshell, Lehrman acknowledged that it had been as much a statement of faith as a scientific position. Nevertheless, after what amounted to an apology to Konrad Lorenz, he did not disavow his basic criticisms, again sprinkling salt on the wound. He admitted that “My critique does not now read to me like an analysis of a scientific problem, with an evaluation of the contribution of a particular point of view, but rather like an assault upon a theoretical point of view, the writer of which assault was not interested in pointing out what positive contributions that point of view had made”; but he then went on to add, in parentheses, that “this would be an appropriate point for me to remark that I do not now disagree with any of the basic ideas expressed in my critique” (Lehrman 1970, p. 22).

“INNATE” OR NOT “INNATE”? THE QUESTION

Of Lehrman’s main points, the most crucial is his insistence that classifying behaviors into ‘innate’ and ‘non-innate’, ‘learned’ or ‘non-learned’, or ‘acquired’ and ‘inherited’ is counterproductive because it doesn’t tell us anything about how behavior actually develops; he asserted that it may even be harmful by distracting us from trying to find out more about the developmental process. Of course if this point is true, it is an equally valid criticism of a geneticist who defines a trait as *genetically* determined, like eye color, or resistance to a disease. But Lorenz had more philosophical issues in mind when he insisted on the value of innateness concepts, perhaps so obvious to him that he found them hard to articulate persuasively. In an attempted rebuttal, he argued that innate and learned behavior can be distinguished by the different sources of information on which their ontogeny is based (Lorenz 1965). Unfortunately, many found his response rather vague and unconvincing, and it failed to resolve the dilemma to anyone else’s satisfaction. Meanwhile, there had

been developments on other fronts.

Soon after I began my doctoral studies in Cambridge, there was a visit by the Canadian physiological psychologist Donald Hebb (Fig. 1) from McGill, still famous today for the ‘Hebb synapse’. His 1949 book on *The Organization of Behavior* touched on many developmental questions, and as a student I was able to listen in on some of the discussions he had with Thorpe and Hinde. I found his take on these issues about instinct and learning illuminating and refreshing. He completely acknowledged the dilemma upon which Lehrman was so completely focused, and agreed that “we are no farther forward by coining a new name for instinctive behavior”. Reflecting on the many problems that arise, he pointed out that “we are involved here in the difficulties of the constitutional-experiential dichotomy. We must distinguish, conceptually, the constitutional factor in behavior from the experiential, but there is presumably no mammalian (or avian) behavior that is uninfluenced either by learning, or by the constitution that makes some learning easy or inevitable” (Hebb 1949, p. 166).

But interestingly, like Lorenz, Hebb still found it heuristically valuable to distinguish between instinctive behavior and learned behaviors. He took this position even though he insisted that when we adopt a developmental approach, which is surely what Tinbergen was advocating, the instinctive/learned distinction loses some of its logical underpinnings (Hebb 1958). Thus, Hebb continued to express Lehrman’s essential point, but in a more balanced way: “In distinguishing hereditary from environmental influence, it is reasonable and intelligible to say that a difference in behavior from a group norm, or between two individuals, is caused by a difference of heredity, or a difference of environment; but not that the deviant behavior is caused by heredity or environment alone” (Hebb 1953, p. 47).

GENETICISTS AND INNATENESS

Meanwhile, geneticists were equally concerned about the need for a deeper understanding of the interplay of nature and nurture, long acknowledged



J.B.S. Haldane (1892 - 1964)

Ivan Ivanovitch Schmalhausen
(1884 - 1963)Mary Jane West-Eberhard
(1941 -)William Homan Thorpe
(1902 - 1986)

Fig. 2 – Haldane, Schmalhausen and West-Eberhard have all brought genetic insights to bear on the innateness controversy. Thorpe launched the era of modern research on birdsong.

as one of their central problems. In my undergraduate days at the University of London, I was lucky enough to hear the lectures of the great geneticist J.B.S. Haldane (Fig. 2). With characteristic lucidity Haldane (1946) pointed out that the positions of theoreticians and of experimentalists on the subject of nature and nurture are rather different: ‘‘We can only determine the differences between two different genotypes by putting each of them into a number of different environments’’.

Around this same time, a related point of view found expression from the Russian population geneticist Ivan Ivanovitch Schmalhausen (Fig. 2) in his book on *Factors of Evolution*. This book had an interesting history. It was written in 1943, but because of his opposition to Lysenko it was vetoed by Stalin; it was finally published in Russian in 1947 and only in 1949 in English. The translation was

spurred on by the professional encouragement of Theodosius Dobzhansky at Columbia in New York. In his book, Schmalhausen took it for granted that the environment is a necessary part of every developmental interaction, but then he added a critical point: ‘‘What matters in this interaction between organism and environment is that the morphogenetic reaction is typical of the organism under given conditions[...] The organism itself determines its relationship to its environment, thus protecting itself against some influences and utilizing others. Every species profits from environment in its own way and responds to changes in environment in different ways’’ (Schmalhausen 1949). Evidently it was clear to Schmalhausen, as it was to Haldane, that although the interplay between nature and nurture during development is inescapably ubiquitous, nurture plays a more dominant role with some traits than others, bringing us closer to what Lorenz had in mind. A term like ‘innate’ serves to capture at least something of that distinction.

In spite of the inexorable nature/nurture duality, people still cling tenaciously to words like ‘instinctive’ and ‘innate’. I think they do so because these terms serve a useful if somewhat limited purpose as labels for behaviors in which genetic factors play an especially dominant role during development. Even Hebb (1949), ever cautious about its limited explanatory value, regarded the term ‘instinctive’ as heuristically useful: ‘‘This is behavior in which the motor pattern is variable but with an end result that is predictable from acknowledgment of the species, without knowing the history of the individual animal. This class of behavior must be recognized’’ (Hebb 1949, p. 166).

If only Hebb’s temperate views had prevailed over the more inflammatory approach of Lehrman, the history of the innateness concept might have proceeded very differently. Instead, the whole issue was thrown into a turmoil from which, I believe, it has taken several decades to recover. Under the influence of W.H. Thorpe (Fig. 2), research on birdsong was one of the few areas of animal behavior in which some creative balance was maintained. Today a new

era is dawning; finally we are now able to manipulate experimentally all components of the developmental equation. The complexity is awesome, but progress is being made, and we can hope that before too long the study of behavioral development will stand shoulder to shoulder with other approaches to animal behavior.

PHENOTYPIC PLASTICITY

Another important issue in the study of instinctive behavior is the question of stereotypy. Does stereotypy imply innateness? Does behavioral variability and plasticity justify a judgment of ‘non-innateness’? One valuable step forward in dealing with this question, building on Schmalhausen’s ideas, is the growing recognition that the concept of ‘phenotypic plasticity’ is relevant to the study of behavioral ontogeny. Entomologist and population geneticist Mary Jane West-Eberhard (Fig. 2), whose book on *Developmental Plasticity and Evolution* was just published (West-Eberhard 2003), defines phenotypic plasticity as “the ability of a single genotype to produce more than one alternative form of morphology, physiological state, and/or behavior in response to environmental conditions”. The concept of phenotypic plasticity serves to remind us of two things. First, one and the same genotype can encode instructions for the development not just of a single phenotype, but of several, even many. The choice of which ontogenetic trajectory a given organism will pursue depends on the environment experienced. Second, and equally important, the genotype has a direct and powerful influence on which aspects of the environment are most potent in eliciting changes in patterns of gene expression, recapturing the essence of the Lorenzian concept of ‘innate release mechanisms’. From an evolutionary viewpoint, what an organism responds to is just as important as what it does. So, contrary to what Lehrman implied, a discovery that an environmental change can modify the trajectory of behavioral development does not automatically provide ammunition for an anti-genetic argument, however illumi-

nating it may be from an ontogenetic viewpoint. The genotype exerts a strong influence on the specific attributes of environmental change that elicit different kinds of behavioral responses. Behavioral plasticity does not in itself imply that genetic influences are absent.

I argue that concepts of innateness do have value. But some will always object to notions of innateness in principle. One reason may be a deep-rooted belief that whenever you invoke nature in discussions of behavioral development, there is an implied commitment to total, unequivocal predestination. It is as though if you use the term ‘innate’ you automatically believe in the inevitable emergence of a unimodal, stereotyped behavioral phenotype. As I have indicated, this is simply a mistaken view. Notions of innateness allow for an infinite range of options for developmental plasticity, adaptive or otherwise. In fact, in the varied environments found in nature, it would be astonishing if the same genotype yielded only one morphological or behavioral phenotype. In some degree, phenotypic plasticity may prove to be ubiquitous.

For a full account of the basic principles, consult West-Eberhard (1989, 2003). I present a few examples as illustrations. A classic case with behavioral connotations is caste determination in social insects; the morphology and behavior of workers is tightly controlled by their environments; the presence of a queen, egg size, nutrition, and temperature all trigger different growth programs (Hölldobler and Wilson 1990). There are endless examples of adaptive environmentally triggered changes in insect life cycles. Some butterflies have seasonally-distinct morphs, once thought to be different species, displaying adaptive contrasts in morphology and behavior; they are actually alternative phenotypes triggered typically in the tropics by seasonal temperature changes and in temperate regions by changes in photoperiod (Shapiro 1976). Even within a species there can be genetically determined variations in the photoperiod specifications for the control of diapause, depending on latitude (Tauber et al. 1986). A wonderful case of phenotypic plasticity is the moth

Nemoria in which the larva mimics either a catkin or a twig. The two morphs differ radically in appearance and behavior, and larvae displaced on an oak tree actively relocate, either on catkins or twigs. The alternative growth patterns are triggered by specific aspects of diet, especially the concentration of tannins (Greene 1989). There are many cases of apparent phenotypic plasticity in vertebrates (West-Eberhard 2003). In fish, amphibians, birds, and mammals, intraspecific variation in patterns of social organization is apparently cued by such experiential factors as population pressure, sex ratio, food availability, and predation (Lott 1991). Some degree of genetically preordained and environmentally triggered phenotypic plasticity may turn out to be a virtually universal feature of living things (Raff and Kaufman 1983).

BIRDSONG AND THE INSTINCT TO LEARN

West-Eberhard (2003) argues persuasively that the developmental plasticity of behavior can be accommodated under the same conceptual umbrella as the development of physiology and morphology; specific cues from the environment, physical or social, engender changes of state of the organism; these changes in turn modify patterns of growth, especially in the nervous system, changing motor patterns, and inducing new patterns of responsiveness to external stimuli. Even learning, the most specialized manifestation of developmental plasticity, can be viewed as a form of cueing by particular external stimuli, novel in their particulars, but interacting with genetically based sensory and motor predispositions. The notion of ‘instincts to learn,’ sought to capture the essence of this interplay of nature with nurture that underlies so many cases of learning under natural conditions (Gould and Marler 1984, 1987). Even something as complex as song learning in birds could conceivably be based on an ‘instinct to learn’, with auditory song experience operating, not with a ‘tabula rasa’, but with extensive innate knowledge about the species’ song already encoded in the brain (Marler 1997). Song learn-

ing may qualify as an example of phenotypic plasticity. But the complications of song development also serve well to illustrate the potential minefield that confronts us if we label behaviors as instinctive or acquired, and the use of that label as a basis for thinking about behavioral development.

We do indeed speak readily of bird songs as innate or learned. Songs of the North American flycatchers (family Tyrannidae) are clearly innate; the song of the Eastern Phoebe *Sayornis phoebe* develops normally in a bird raised in social isolation (Kroodsma and Konishi 1991). On the other hand, songs of sparrows (family Emberizidae) are learned; in nature songs develop very differently from when male sparrows are raised out of hearing of their own kind. Because sparrows copy tutors in detail, we don’t hesitate to classify these as learned songs and this classification may serve some value in preparing us for the likelihood that patterns of natural song variation will be very different in sparrows and flycatchers. But the more you think about it the less straightforward this labeling procedure really is, raising all the questions that Lehrman was so concerned about. If we conclude that flycatcher songs are innate, and sparrow songs are not innate, does it follow that concepts of innateness have no relevance at all to song development in sparrows? The answer is unclear. A Song Sparrow *Melospiza melodia* raised in isolation produces an isolate song that is clearly abnormal, but if we examine it closely, there are still quite a few Song Sparrow-like features (Marler and Sherman 1985). It has several parts, like normal song, with a pure tonal quality and a normal overall duration (Fig. 3). What do these normal features of isolate song represent? Are they innate? If so, how should we interpret the abnormal aspects of isolate song? Perhaps it would be useful to regard song as a kind of mosaic and to classify some features as innate, and others as not innate?

We get another perspective on this question by comparing Song Sparrows with a second species, the Swamp Sparrow *Melospiza georgiana*, which has a much simpler song. Again, isolate Swamp Sparrow song is abnormal. It is simpler, with a

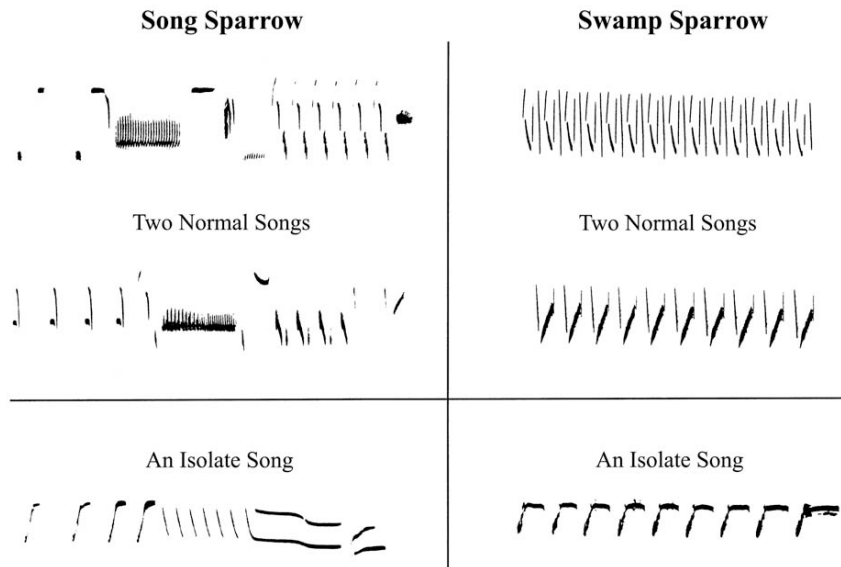


Fig. 3 – A comparison of songs developed in nature and in social isolation by two sparrows, the Song Sparrow *Melospiza melodia* and the Swamp Sparrow *Melospiza georgiana*.

less complex syllable structure, and a slower tempo (Fig. 3). These are all characteristics shared with isolate Song Sparrow song. So in both species song characteristics like syllable complexity and tempo are developmentally plastic. But there is another side to this coin. If we make a 4-way comparison, between natural and isolate songs of both species, we find something interesting. Despite the abnormalities of their isolate songs, the two species are nevertheless easy to tell apart.

Some of the song features in which the two species differ are immediately understandable: they differ in normal song, and remain unchanged in isolates (Fig. 4). These are features like song duration and over all frequency range, and if we restricted our attention solely to them, we could conclude that sparrow songs are innate. But we know that other features of these 'learned' songs develop abnormally in isolation. Clearly some song features are less fixed than others, less resistant to change, more subject to nurture than to nature. As already mentioned, we could classify features that resist change, as innate, and those more readily changed as not innate, using potential mutability as a yardstick. Song fea-

tures do indeed differ in their mutability, and two that have been shown to be especially mutable in sparrows and other birds are song repertoire size, and the number of notes in the song (Fig. 5). Both shrink drastically in the songs of isolates, leading us to conclude that song repertoire size and note number are not innate.

But if we now compare these features of isolate songs across species we find something surprising. Despite the abnormalities in the number of notes in songs in both species, with the slower tempo, and with note durations and inter-note intervals drastically lengthened, species differences persist. If we count the total number of notes, the average is shorter in Swamp Sparrows than in Song Sparrows, to the same degree as in normal song. The comparison of song repertoire is even more striking. A wild male Song Sparrow has a large repertoire of 10 or so song types, a male Swamp Sparrow's is smaller, comprising three or so songs. In both species, repertoires shrink to about half the normal size in isolates; but despite this shrinkage, isolate Song Sparrow repertoires, at 5 per male, are still three times larger than those of Swamp Sparrows,

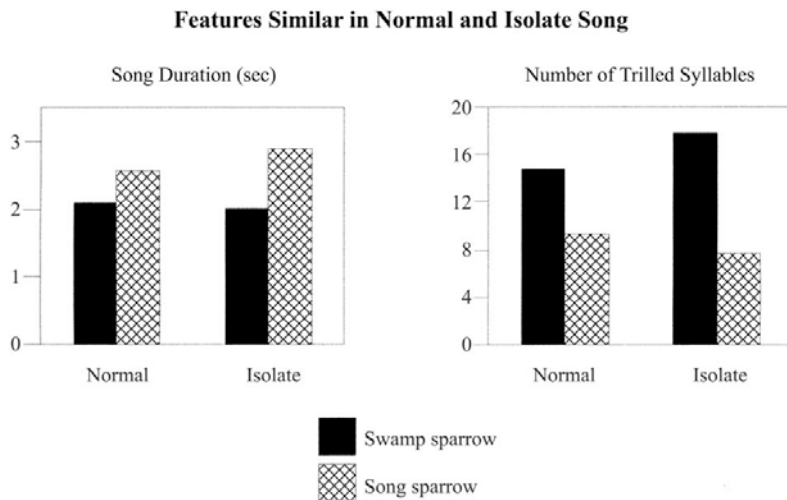


Fig. 4 – Two song features compared in Swamp and Song Sparrows that develop normally in social isolation. Species differences are maintained. From Marler and Sherman 1985.

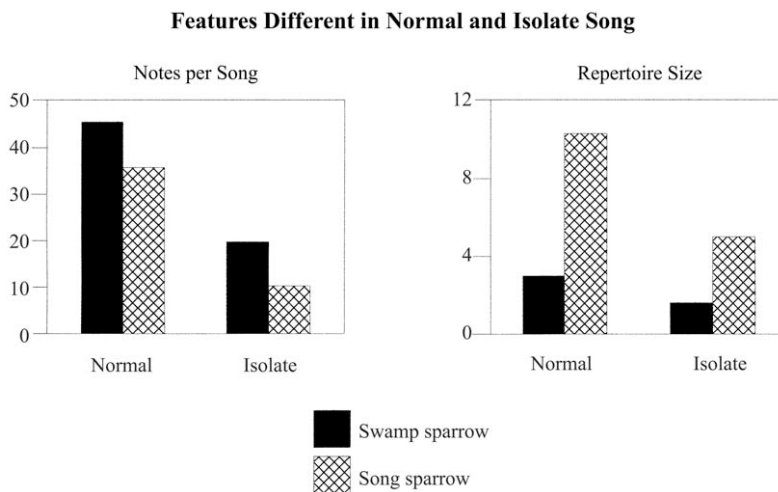


Fig. 5 – Song features that develop abnormally in isolation still display species differences like those found in nature. From Marler and Sherman 1985.

at an average of 1.6 (Fig. 5). So song features that are developmentally labile can nevertheless still display species differences – differences that must be genetically based. Should we then classify repertoire size and note number as learned or as innate? Clearly neither conclusion is satisfactory. It is obvious that the classification into innate or learned, or into more innate and less innate just breaks down.

The interrelationships between nature and nurture are simply too complex and intricate and interwoven to be amenable to an either/or classification.

CONCLUSIONS

So with this brief overview of song learning, we find ourselves confirming what Lehrman (1953) asserted 50 years ago. If you are interested in mech-

anisms of behavioral development, classifying behaviors in a dichotomous fashion like this is no help at all. However, I should also add that it is not clear to me that it is worth getting so upset about. The habit of labeling behaviors in this fashion is so deep rooted that we will probably never succeed in eradicating it. And it does have some general value in placing behaviors on a variability continuum, with behaviors perhaps more 'nurture-dependent,' more changeable and variable at one extreme, and behaviors that are more 'nature-dependent,' more stereotyped and more resistant to change, at the other.

So can we regard the nature/nurture controversy as having been laid to rest? The problem is that we still have extraordinary little in-depth comprehension of the interactions between genotype and environment that underlie the development of behaviors. I like to think that the notion of 'instincts to learn' at least points us in the right direction, but in fact, the enterprise of coming to understand them has hardly started. So this fourth area of behavioral research that Tinbergen was so anxious to bring to our notice, still remains a major challenge for future bioacousticians, and all other students of behavior.

In embarking on this grand endeavor, it will behoove us to bear in mind any lessons we can glean from past history. Those who resist the invocation of genetic contributions to behavioral development, may still need to be reminded that involvement of the genome need not imply a commitment to stereotyped behavior. In fact, as Waddington (1957) once pointed out, the stereotypy of some behaviors could itself actually be deceptive. It could turn out that the underlying potential for flexibility is just as great with stereotyped behavior as with variable behaviors, but is masked by added mechanisms that detect and correct for the perturbations to which a developing organism must always be subject. This is a theme that is currently getting much attention in birdsong studies, as fully crystallized adult song turns out to be more subject to modification than had ever been suspected, if you perturb the feedback controls (Nordeen and Nordeen 1992, Okanoya and Yamaguchi 1997, Woolley and Rubel 1997, Leonardo

and Konishi 1999).

Above all, we must acknowledge the likelihood that genomes have evolved ways to cope with changing environments. This is necessary if we are ever to understand the genetics of behavior. The selective stakes for coping successfully with different environments are so high that pressures for the evolution of genome-controlled strategies for adaptive interaction with changing environments must be intense. And we must not forget that 'innate' responsiveness to particular environmental cues, central to the ethology of Konrad Lorenz, often highly specific, is likely to have evolved with an inevitable influence on the choice of alternative strategies. Once again, we confront the universal duality of nature and nurture but progress is being made. In many ways behavioral scientists have led the field in analyzing and understanding the contributions of 'nurture' to ontogeny (Gottlieb 1976, 1992), even though the role of 'nature' has been neglected. Now that the methods and concepts of modern genetics have become so sophisticated, the 'nature' side of the equation is equally tractable. Our hope for the future lies in combining these approaches to create a unified theory of behavioral development in which the critical roles of the genome and the environment are both acknowledged to the full.

RESUMO

O conceito de inato estava no cerne da abordagem de Darwin ao comportamento assim como no das teorias etológicas de Lorenz e, pelo menos inicialmente, de Tinbergen. Depois, Tinbergen deu uma reviravolta e, durante mais ou menos vinte anos, o termo "inato" tornou-se altamente suspeito. Tinbergen atribuiu sua mudança à famosa crítica de Lehrman, em 1953, segundo a qual classificar comportamentos como inatos não traz informação alguma a respeito de seu desenvolvimento. Embora muitas das críticas de Lehrman sejam relevantes, tentarei mostrar que a mudança de enfoque também gerou sérios equívocos que acabaram prejudicando o progresso da pesquisa sobre o desenvolvimento do comportamento. O conceito de "instintos para aprender", reforçado por teorias recentes de geneticistas a respeito da plasticidade fenotípica, abre um caminho para a superação de algumas das controvérsias

que Lehrman originou. Estudos em bioacústica, em particular sobre a aprendizagem do canto em aves, confirmam alguns dos temores de Lehrman a respeito do termo “inato”, mas também mostram que ele restringiu, sem discernimento, a relevância da determinação genética. O progresso espetacular da genética molecular e da genética do desenvolvimento fornece a base para uma melhor apreensão da complexidade existente até nas noções mais simples de comportamento inato, o que é necessário para que possamos entender a ontogênese do comportamento.

Palavras-chave: inato, aprendizagem do canto, plasticidade fenotípica, genética comportamental, as quatro perguntas de Tinbergen.

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