Biological Theory (2024) 19:137–149
https://doi.org/10.1007/s13752-024-00459-3

CLASSICS IN BIOLOGICAL THEORY: ENGLISH TRANSLATION

A Discussion on Instinct, Paris, 1954

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Accepted: 29 January 2024 / Published online: 21 February 2024

Abstract

The publication of Daniel Lehrman's 1953 paper, "A Critique of Konrad Lorenz's Theory of Instinctive Behavior," (*The Quarterly Review of Biology* 28(4):337–363) exposed a gulf between comparative psychologists and ethologists regarding the concept of instincts. At the center of this debate was a rivalry between T. C. Schneirla—Lehrman's doctoral advisor—and Konrad Lorenz. While Schneirla maintained that the concept of innate instincts mischaracterized developmental processes, Lorenz maintained that innateness was essential to understand the evolution of behavior. A year after the publication of Lehrman's paper, the Singer-Polignac Foundation organized a small conference where leaders in evolutionary biology, ethology, behavioral physiology, and comparative psychology met to discuss the concept of instinct and innateness. The result of this meeting was the publication of the book *L'instinct dans le comportement des animaux et de l'homme* (M. Autuori et al. (1956) Masson, Paris) in which each conference participant submitted a chapter that was followed by a discussion among the participants. Here I review the historical context surrounding this conference with a republishing of the commentary on Schneirla's chapter, "Interrelationships of the 'Innate' and the 'Acquired' in Instinctive Behavior." Originally published in English, German, and French, the discussion is included here with a new translation into English for the first time. A companion article (this issue; G. M. Kohn (2024) "Revisiting T. C. Schneirla's 'Interrelationships of the "Innate" and the "Acquired" in Instinctive Behavior' (1956)") discusses and makes available Schneirla's complete paper.

Keywords Comparative Psychology · Development · Ethology · Innate · Innateness · Instinct · D. Lehrman · Nativism · T. C. Schneirla

> *How behavior develops is the problem to solve, rather than distinguishing between what is innate and what is acquired.*
>
> —*T. C. Schneirla*

Introduction

In 1954 a group of American comparative psychologists traveled to Paris to meet their European ethologist counterparts. The aim of the meeting was to discuss the concept of instinct. Tensions between the Americans and Europeans were high. The publication of Daniel Lehrman's paper "A Critique of Konrad Lorenz's Theory of Instinctive Behavior" in 1953 had unexpectedly put the ethologists on the defensive (Lehrman 1953). Lehrman's paper critiqued some core assumptions of the classical ethological program. It claimed that a critical feature of instincts—that they were *innate*, and thus developed independently of an individual's experiences—was based on a mischaracterization of behavioral development and the role of experiences in ontogeny.

The Paris meeting was sponsored by the Singer-Polignac Foundation and would be the first time both groups met since the paper was published. It would be the first of three meetings that sought to bridge the divide over the concept of instinct, and eventually create a new science of animal behavior. One outcome of the Paris meeting was the publication of the book *L'instinct dans le comportement des animaux et de l'homme* (Autuori et al. 1956). Each of the participants contributed a chapter, and after each chapter the participants wrote a brief "open peer commentary" in

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response to the chapter, which was followed by a response by the author.

This exchange between the ethologists and comparative psychologists provides a window into the debate over instincts at a critical period in the history of animal behavior studies. At the center of this debate were two figures, Theodore C. Schneirla and Konrad Z. Lorenz. Schneirla, as Lehrman's doctoral advisor, was largely seen as the foremost skeptic of the innate–acquired dichotomy. Despite this, Schneirla's article, "Interrelationships of the 'Innate' and the 'Acquired' in Instinctive Behavior" (Schneirla 1956) was his first full-length piece to specifically deal with the innateness concept. While this article is revisited in depth in this issue (Kohn 2024), the commentary after the article showcased clear differences between the ethologists and comparative psychologists that continue to be relevant to modern debates in the fields of behavioral ecology, psychology, behavioral genetics, and animal behavior. To help reintroduce this commentary (Schneirla 1956, pp. 439–452), it is reprinted it in its entirety in this issue of *Biological Theory*, with an English translation of the original French and German text.

The entrenchment of the innate–acquired dichotomy in the behavioral sciences is highlighted in many of the participants' responses. In particular, two themes stand out in contention between the different camps: (1) what the existence of highly structured behavior tells us about development and (2) what characterizes causality in development.

Throughout the discussion many participants reiterate their views that stereotyped and complex behaviors—especially occurring early in life—can only be interpreted through the lens of innateness. This can be seen clearly in the responses of Lorenz and Deleurance. Lorenz references a study by Paul Weiss where limb buds of *Ambystoma* salamanders were artificially translocated across the body but retain their original motor patterns. Another example was the presence of eye cleaning behavior in cyclorrhaphan flies despite developing without a head.

When discussing coitus behavior in rats Koehler finds it difficult to see how rats could "ever learn such an immensely complex and coordinated behavior." Deleurance states that the organized behavior of young *Polistes* wasps could not be learned via the traditional Pavlovian processes, and thus are not acquired. Such responses seem to restate the learned–innate distinction while leaving the broader developmental approach Schneirla proposed unaddressed. For instance, Koehler's defense of isolation techniques still maintains that experiences should be discounted if a behavior occurs after isolation, while avoiding the examples of experience dependence in isolated animals discussed by Lehrman and Schneirla.

In his response to Lorenz, Schneirla discusses the conceptual ambiguity of instinct, which he calls "an abstraction" of "heuristic value, but which may be only relatively different from other actions more variable in their form." By centering ethology on the strong separation between instinctive and non-instinctive behavior, the ontogenetic processes underlying behavior become obscured, as instinctive behaviors are assumed to have a unique innate role in comparison to non-instincts.

Schneirla urges the participants to adopt a border perspective, one that moves beyond instincts, learning, and innateness to consider all causal factors specific to the development of a behavior. He asserted that the "interactions of organism and developmental context are highly complex and demand analytical study," and the assumption of innate or acquired obscure these efforts, leading to a misinformed picture of developmental *causes*.

Developmental causes occupy a central point of disagreement between the participants, with the comparative psychologists (Lehrman, Schneirla) focusing on the distributed nature of causes across the organisms and its environment, while the ethologists (Lorenz, Koehler) emphasized the privileged role of genetic causation. As Lehrman suggests, this disagreement may stem from the way that developmental research programs are characterized. The ethologists emphasize the importance of detailed descriptions of animal development, noting when specific behaviors emerge, and describe the structure of those early behaviors in detail. In contrast, the comparative psychologists seek to understand the specific causal interactions necessary for the emergence of behavior. It's the difference between cartography and navigation. To the ethologist a developmental research program is centered on building developmental maps that chart the entirety of species-typical behavioral development, while the comparative psychologist focuses on navigating the details that govern how specific behaviors emerge and change.

At multiple points Schneirla and Lehrman show examples of the diverse ways that experiences shape developmental outcomes beyond traditional learning. These contexts include self-stimulation, constraining influences during critical periods, and shifts in physiological pathways in response to nonobvious environmental factors. Their main point is that the mere existence of a structured behavior does not in itself say anything about developmental causes, especially the role of experiences in developing that structure.

This point is rejected by some and adopted by others. Koehler reiterates the importance of "Kaspar Hauser-style" (a reference to a famous feral child episode where an individual claimed to have been raised in a darkened room) isolation studies where early aspects of development are changed to identify innateness. Haldane uses the example of burning paper to show that it is the flame (an analogy for genes), and not the qualities of the paper (an analogy for the rest of the organism) that cause it to burn. Schneirla responds by claiming that to understand the burning of paper we cannot discount the qualities of the paper that give it the capacity to burn along with the context where the burning occurred. He states, "we must consider not only kind of paper but also how it has been prepared for the test, also the match, atmospheric conditions, and so on."

Schneirla's response foreshadows what would later become developmental systems theory. His responses highlight that there is no privileged level of causation in development, and as such, research should be open to the possibility that all organism–environment interactions could be causal factors in producing that behavior. Despite claims by both Kohler, Lorenz, and others that his perspective ignores hereditary factors in behavior, Schneirla reiterates that hereditary factors only make sense in the context of developmental interactions. He states that factors such as genes must be considered "as inseparably merged from the beginning of development in what I have called the systems of 'intervening variables.'"

One ethologist was willing to endorse the influence of experience on all behaviors, including instinctive ones. Desmond Morris was a student of Nikolaas Tinbergen. Along with Lorenz, Tinbergen is widely considered the other founder of ethology. However, unlike Lorenz, Tinbergen came to agree with the perspective of Schneirla and Lehrman. In Morris's response we see an agreement that the innate–acquired dichotomy, "as used by ethologists, in the past, has been most unfortunate." He proposes two broad types of experiences—one at the level of the species and the other at the level of the individual—that might create discontinuities between species-typical and individual behaviors. His suggestion allows for the separation of species-typical "instinctive" behaviors so important to the ethologists, without the assumption of innateness. This theme eventually became a cornerstone in the science of developmental psychobiology, and further research done by both Schneirla, Lehrman, Gottlieb, West, and their students would come to focus on how species-typical developmental contexts, called ontogenetic niches, are necessary to understand the ontogeny of species-typical behavior (Schneirla 1966; Beer et al. 1986; Gottlieb 1997; West and King 2008).

In the years following the Paris meeting, the controversy over the nature of instinct cools. A friendship between Tinbergen and Lehrman leads Tinbergen to abandon using the term innateness when discussing instincts. Two subsequent meetings, a Macy Foundation Conference in Ithaca, New York, and an International Ethological Conference in Groningen, Netherlands, both center around Lehrman's paper and lead to a greater reconciliation between comparative psychology and ethology. Schneirla continues to praise Lorenz's detailed observations and love of natural history, and while Lorenz never fully accepts his critique, he does favorably cite Schneirla in one of his last books (Lorenz et al. 1991).

Nonetheless, debates over innateness are experiencing a revival. Recent discussion over the role of experiences in the development of behavioral and linguistic abilities shares many parallels with the debates highlighted here (Zador 2019). I hope that by looking at the historical trajectory of the innate–acquired dichotomy we can better assess if current discussions are covering new ground, or simply rehashing old tropes.

Biographical Sketches of Participants

Theodore Christian Schneirla (1902–1968) was born to celery farmers in Bay City, Michigan, and received his bachelor's, master's, and PhD from the University of Michigan. At the University of Michigan he investigated maze learning behavior and orientation in ants under the supervision of comparative psychologist Dr. John Shepard. After graduating Schneirla took a professorship at New York University in 1928, but also spent time at the University of Chicago as a National Research Council fellow working with Dr. Karl Lashley. During his time in Chicago he befriended Dr. Norman Maier, which led to the publication of Schneirla's book *Principles of Animal Psychology*. This book (Maier and Schneirla 1964) presented a new vision for comparative psychology outside the dominant behaviorism of the time, one that focused on the development, evolution, and structure of species-typical behaviors across species. In 1932 he took the first of many trips to Barro Colorado Island in Panama to study the social organization of army ants, investigating the factors causing the nomadic to stationary transitions in army ant colonies. While this transition was previously considered to be driven by innate mechanisms, Schneirla showed how they were driven by an interacting network of social, physiological, and environmental causes. Such studies were later expanded to encompass numerous different ant species from across the globe.

In 1943 Schneirla was invited to become a member of the Department of Animal Behavior at the American Museum of Natural History in New York, eventually becoming permanent staff and head curator of the department in 1947. Here he mentored many leading comparative psychologists including Daniel Lehrman, Ethel Tobach, Howard Toppoff, and Jay Rosenblatt. During this period, he formulated his theory of approach–withdrawal as a shared characteristic of all behavior and introduced a novel concept of integrative levels to comparative psychology. Schneirla also expanded his empirical studies beyond ants, looking at the development of social relationships in mammals. His emphasis on taking a developmental perspective when investigating animal behavior laid the foundation for developmental systems theory. He died suddenly in 1968, and his book *Army Ants* was published posthumously with Dr. Toppoff (Schneirla 1971).

Konrad Zacharias Lorenz (1903–1989) is considered one of the founders of classical ethology. Born in 1903, he was raised between Altenberg and Vienna, Austria. He spent a year at Columbia University in 1922 as a premedical student, but then returned to Austria, graduating from the University of Vienna as a doctor in medicine in 1928 and earning a doctorate in zoology from that institution in 1933. Throughout his studies Lorenz kept a large number of domestic and wild animals in his Vienna apartment. During his doctorate he studied the social behavior of jackdaws, writing "Companions as Factors in the Birds' Environment" in 1935, where he described imprinting behavior in detail. He met Nikolaas Tinbergen in 1936, forming a lifelong friendship.

In the late 1930s Lorenz published a series of studies that helped characterize the concept of instinct (Lorenz 1970). In 1937, he published "The Establishment of the Instinct Concept" which outlined his ideas on instinct, and in 1938 he published "Taxis and Instinctive Behaviour Pattern in Egg-rolling by the Greylag Goose" that showed how instinct could be applied empirically (Lorenz and Tinbergen 1970). He joined the Nazi party in 1938 and shifted his political views to support the ideology of the state, writing papers in support of eugenics. Shortly after becoming a professor of psychology at the University of Königsberg in 1940, he was assigned to the army as a medic, but became a Soviet prisoner of war in 1944. During his internment he drafted what would later become his philosophically focused book *Behind the Mirror: A Search for a Natural History of Human Knowledge* (Lorenz 1977). In 1958 he moved to the Max Planck Institute for Behavioral Physiology in Seewiesen, Austria, and continued his work on imprinting in geese. In 1973 he won the Nobel Prize for medicine with two other founders of ethology, Nikolaas Tinbergen and Karl von Frisch, and then retired to do research in Grünau im Almtal, Austria.

Otto Koehler (1989–1974) was a pioneering German ethologist and friend to Konrad Lorenz. Born in 1889 in Innsbruck, Prussia, to a Lutheran minister and his wife, he went on to study history and mathematics at the University of Freiburg. Here he attended lectures by August Weismann and Waldemar Schleip that led to an interest in zoology. In 1908 he transferred to the University of Munich and received a doctorate in zoology. After graduation he briefly worked with Karl von Frisch. Koehler opened a laboratory in Anatolia during WWI and after a brief stint as a British prisoner of war became an associate professor in the University of Munich in 1923 and then the director of the Natural History Museum at the University of Königsberg in 1925. His behavioral research spanned investigations of taxis behavior in Paramecium, to the breeding biology of plovers, to the counting ability of birds, and song learning abilities in passerines. He was among the first individuals to ring birds for individual identification, and one of the first ethologists to recognize the importance of video recordings for the study of behavior. Koehler was also a pioneer in the use of experiments to conduct comparative research on behavior and cognition.

Desmond Morris (1929–present) is an ethologist, author, and television producer widely known for writing the controversial *The Naked Ape* (Morris 1994). He was born in Wiltshire, England, in 1933. He developed a keen interest in natural history and art from an early age, and became a member of the British Army, teaching art at the Chiseldon Army College. After WWII he studied zoology at the University of Birmingham and in 1951 started his doctorate under the supervision of Nikolaas "Niko" Tinbergen at Oxford, studying the courtship behavior of ten-spined sticklebacks. After graduating he stayed at Oxford and conducted groundbreaking work on the behavior of Estrildid finches, writing one of the first behavioral papers on the behavior of the zebra finch (*Taeniopygia guttata*) before it became a model species. In 1956 he started working for the Zoological Society of London, conducting research on primate cognition and producing the television shows *Zoo Time* and *Life in the Animal World*. During this period he also wrote numerous popular books on animal behavior, including *The Naked Ape*. He returned to academia in 1973 to work with Tinbergen and produced many documentaries including *The Human Animal*. He is also an accomplished surrealist painter and has had his work shown in galleries all across the world. He currently lives in Ireland.

John Burdon Sanderson Haldane (1892–1964) was a British-Indian evolutionary scientist credited with helping to forge the modern synthesis and population genetics. Son of the physiologist John Scott Haldane, he grew up performing experiments in his father's laboratory. He studied mathematics and the classics at Oxford but became interested in genetics despite having no formal education in biology. After serving in WWI, he was hired at the New College in Oxford, moving to Cambridge University in 1923, and then to University College in London in 1933. In 1956 he moved to India to work for the Indian Statistical Institute in Kolkata.

His contributions to modern science are vast and span the gamut from developing the field of population genetics to producing important work on the origin of life, genetic linkage, and animal behavior. His insights led to major advances in understanding kin selection, neutral evolution, the importance of body size, and the concept of Darwinian fitness. He died in India in 1964.

Helen Haldane-Spurway (1915–1978) was a British biologist who specialized in genetics. She obtained her doctorate in 1938 under the supervision of J. B. S. Haldane at the University College of London, whom she later went on to marry. They moved to India in 1957 to work for the Indian Statistical Institute in Kolkata. She was originally interested in the study of parthenogenesis, and suggested that guppies reproduce parthenogenetically. She also had a keen interest in animal behavior and domestication, publishing a paper in 1955 that expanded on Konrad Lorenz's theories of domestication (Spurway 1955) and another on the comparative breathing behaviors (Spurway and Haldane 1953). During her time in India the bulk of her research focused on the genetics of the silkworm *Antheraea mylitta*, but she also conducted research on animal behavior, studying the communicative behavior of *Apis mellifera*. She died in Hyderabad, India, in 1978.

Edouard-Philippe Deleurance (1918–1990) worked in the "Laboratoire d'évolution des êtres organisés" at the Université de Paris under the supervision of Pierre Paul Grasse (organizer of the Paris Conference in 1954) and described himself as a "comparative psychophysiologist." He came to run the Animal Behavior Department at the Centre National de Recherche Scientifique (CNRS) in Marseille. Deleurance's research at CNRS focused on integrating ethological and neuroendocrine perspectives on the nesting behavior of *Polistes* wasps, and an investigation into the hormonal mechanisms that initiate and regulate the molting of insects. He was vocal in arguing for moderation in the use of anthropomorphic concepts to describe seemingly human-related phenomena in animals. For instance, he was critical of extending the concept of dominance (derived from observations of vertebrates) to explain invertebrate social behavior.

Marc Klein (1902–1975) started his career as a student in Pol Bouin's laboratory at the University of Strasbourg and finished his doctoral degree studying the corpus luteum in rabbits. Klein's work showed that the formation of the corpus luteum was not under the control of the developing embryo, but of the mother, through placental and uterine mechanisms. He stayed at Strasbourg for his entire career, continuing to work in reproductive physiology and extending many of his results in rabbits to other species. During the war Klein worked as an army doctor but returned to the University of Strasbourg in 1940. In 1944, however, he was arrested by the Gestapo and was interned in Auschwitz and Buchenwald for a year. He was able to return to Strasbourg in 1946 and held the chair of the new Department of Medical Biology. His research shifted to studying the neuroendocrine processes underlying morphology, human behavioral genetics, ovarian physiology, and milk secretions. He also maintained a keen interest in the history of science, publishing a book on the history of cell theory (1936).

Daniel Lehrman (1919–1972) was born and raised in New York City, with a childhood marked by his parents' marital problems and poverty. During his teenage years a scoutmaster introduced Lehrman to birdwatching and instilled a deep interest in natural history and avian behavior. He birded with Ernst Mayr and William Vogt in Central Park, and in his teens became a research assistant with the head of herpetology at the American Museum of Natural History (AMNH), Gladwyn Kingsley Noble. Lehrman's first research projects looked at the factors influencing incubation behavior in laughing gulls. However, difficulties at home prevented him from finishing his undergraduate degree at the City College of New York, before he was stationed in Italy as a German translator during WWII. After the war he returned to New York to finish his undergraduate degree and started his PhD under the supervision of T. C. Schneirla at the AMNH's Department of Animal Behavior. His dissertation focused on the feeding behavior of ringdoves (*Streptopelia risoria*).

In 1948 Lehrman gave a talk at the AMNH titled "A Critique of the Lorenz Approach to the Study of Behavior." This talk was a preview for the 1953 publication of "A Critique of Konrad Lorenz's Theory of Instinctive Behavior" (Lehrman 1953). After this period Lehrman participated in various conferences that sought to extend the dialogue and discussions over the concept of instinct with European ethologists and developed a close friendship with Tinbergen. In 1959, Lehrman became a professor at Rutgers University and started the Institute for Animal Behavior. He continued his research on reproductive systems in ringdoves and attracted many pioneering animal behavior researchers to the Institute including Colin Beer, Jay Rosenblatt, Mei-Fang Cheng, George Michel, and Lester R. Aronson. His career was marked with his rivalry with Lorenz, culminating in his 1970 paper titled "Semantic and Conceptual Issues in the Nature–Nurture Problem" that reflected on the continuing innate–acquired controversy (Lehrman 1970). He died suddenly of a heart attack two years later.

Discussion of Innate and Acquired Behavior among K. Lorenz, T. C. Schneirla, O. Koehler, H. Spurway-Haldane, M. Klein. D. Lehrman, D. Morris, E.-P. Deleurance, & J. B. S. Haldane (1954) (with translated passages by Gerd B. Müller and Mathieu Charbonneau)

K. LORENZ. — Professor Schneirla has shown us truly admirable examples of successful analyses of the highly complex behaviors of the army ants. In particular, he convincingly demonstrated the high degree of species-specificity, even for those cases in which multiple individual learning processes, and other—by no means genetically determined—factors contribute to these behaviors. Let us remember, for instance, the images he has shown us of the characteristic distribution patterns of swarming ants of different species. I find myself in agreement with everything he has said in the main section, but in the strongest disagreement with some of the conclusions he draws from this at the end of his manuscript (pp. 14 and 15). Above all, I argue that all the correct observations made in the lecture in no way legitimize the conclusions drawn from them, namely that the designations of "innate" and "acquired" cannot be applied to animal behavior and its organization. This conclusion became possible only because throughout the entire lecture not a single basic instinct-movement was mentioned to which the term "innate" can be justifiably applied. I fully agree with professor Schneirla that the occurrence of clear cases of rigidly deterministic movements is not very frequent. However, it is the task of biology to search for the most basic cases, because all the success depends on the detection of such suitable objects of study. The Mendelian laws were discovered because the pure form of the monohybrid forced the attention of the observer. That from the existence of complex behaviors that represent mixtures of multiple factors professor Schneirla should draw the conclusion that the effects of the innate and of the acquired factors are not separable in principle is as equally inadmissible as when someone concludes from the apparent disorder of hybrids from a [pug] and also a dachshund that the Mendelian laws are invalid.

I come back to the classical examples of purely innate instinct-movements that I have already mentioned in my lecture. I remind you of the head cleaning movements of cyclorrhaphan flies that have hatched headless and start cleaning their eyes, which are still invaginated inside the thorax, at the location at which they should lie if the head had properly emerged. I also remind you of the forelimb buds of Ambystoma, which had been transplanted contralaterally by Paul Weiss, and that would obstinately maintain their original movement patterns throughout the rest of their lives. I could name many equally convincing examples.

If professor Schneirla denies the attribute "innate" to these movement patterns, then I would like to ask him what criteria he would postulate for a behavior in order to concede this term.

All the behaviors that professor Schneirla has recorded conceptually in his lecture indeed include aspects of learning. But I maintain that it is not scientifically legitimate to dogmatically assert the non-analyzability of a term, when the facts downright force the necessity to refine it, and enable further studies. Wherever this is the case, in my opinion it will be our duty to do both, refinement of the terminology and advancement of our studies.

T. C. SCHNEIRLA. — Of course I cannot really believe that Prof. Lorenz agrees with everything I have said in my paper, which is too kind a comment from him, or he wouldn't find it necessary to disagree with the conclusions. This point is difficult to answer satisfactorily, since I think the conclusions follow from the considerations offered in the body of the paper. But the reason may be that I haven't been able here to present enough of the evidence that led me to these conclusions, because time has required a considerable shortening of all parts of the presentation and the omission of much material which would have helped greatly. My ms. can give a better conception of how I appraise the difficult topic assigned to me by Prof. Grassé than this talk from notes can have offered.

Of course we do not find species-typical behavior which might be used as a taxonomic character and yet depends altogether on extrinsic factors. I don't think we will, and haven't predicted it. But I have said that intrinsic factors alone will not account for the development of such behavior or any behavior in any species. I meant to emphasize the impossibility of understanding the result, species-typical behavior, without considering the interrelationships of intrinsic and extrinsic factors from stage to stage. The problem is not only oversimplified but is misrepresented when we try to understand the behavioral outcome in terms of encapsulated endogenous determiners of patterns, independent of, such interrelationships. No proof of "Erbkoordination" in this sense has yet appeared.

Prof. Lorenz says that the gist of the problem of "the innate" concerns the "instinctive movement", and that I haven't considered any such movements. Answering this point is somewhat complicated by the fact that I fear the "instinct problem" cannot be formulated as succinctly and positively as this without omitting and distorting both problems and subject matter. Frankly, I haven't labelled anything as "instinctive movement", because I can't bring myself to accept the concept. The origin of the kind of nuclear movement Prof. Lorenz emphasizes remains to be demonstrated in better studies of ontogeny than we have had on any phyletic level. The "instinctive movement" is an abstraction which he finds convenient and of heuristic value, but which may be only relatively different from other actions more variable in their form. More knowledge of individual differences in similar forms of behavior, as well as intraindividual differences from one situation to another, should help to clarify this matter.

My second main point has been concerned with considering the close and complex interrelationships of extrinsic and intrinsic factors (and their trace effects) in development. This I believe is a better overall way to approach the problem of instinctive behavior. Prof. Lorenz has not accused me of ignoring hereditary factors, and I appreciate this. The critical point is how hereditary influences enter into behavior on each phyletic level, and I believe that we must consider them as inseparably merged from the beginning of development in what I have called the systems of "intervening variables". I haven't ignored the problem of what ethologists call "the instinctive movement", although the impression may have been gained from my failure to use the term. I do not think it can be separated so neatly from other aspects of development on the assumption of an insulated genic-c.n.s. [central nervous system] determination. The question of what we may call nuclear, species-typical movements cannot be left out of any such discussion, but I believe that it is more essentially merged with other problems in development. So I have treated it this way, for example in discussing the head-lunge in the pecking response of certain birds. Kuo's fundamental work shows that for an understanding of species typical movements we must analyse ontogeny from stage to stage of development.

The ethologists' analysis of the so-called "instinctive movement" unfortunately is limited almost entirely to the adult or postnatal condition, and does not base itself on ontogenetic prerequisites. I have suggested in effect that if they went further back they would find processes such as I have discussed in connection with the interrelationships of the maturation and experience variables. His results indicate that at earlier stages there may be aspects of the experience type, often introduced through the organism's own activities, which are not learning but still leave trace effects important for later development. Dr. Lorenz asks why the chick pecks and the nestling young of perching birds gape. I think that when we understand the complexities of ontogeny well enough in the different species the answer may be more apparent. But it seems important that at an early stage the embryo chick's head-lifting movement occasionally is combined with a bill-opening which may be really homologous to the anlage of gaping in the nestling of perching species. If so, what happens later to divert it into a pecking pattern? Comparative analytical studies of the embryonic stages seem necessary. Incidentally, we know the gaping response only in outline and for post-hatching stages. For example, although Tinbergen and Kuenen conclude in favor of innately effective visual releasing stimuli for gaping. Dr. Lehrman suggests on what appear to be good grounds that post-hatching events are responsible for the specificity of these "visual releasers". So in my paper I offer reasons for doubting any clearcut distinction between the innate and the acquired. It is difficult to see how extrinsic influences, through effects such as I have called "experience", can be distinguished sharply from the endogenous processes Prof. Lorenz seems to consider linear consequences of genic factors leading to "instinctive movements".

I have also expressed concern about the fact that the concept of the "instinctive movement" seems to have diverted attention from analysis of interrelationships on different phyletic levels. Not only the ontogenetic origin of such nuclear actions, but also their relation to other aspects of the behavior pattern, may prove very different in the principal phyletic types.

Prof. Lorenz asks what proof I would accept for the IRM [innate releasing mechanism] and the "instinctive movement." As I have suggested, evidence for an encapsulated, strictly central IRM, is incomplete until other conditions intrinsic and extrinsic to the organism have been sufficiently considered. Peripheral processes have been excluded from the determination of fundamental movement systems, I suggest without due cause. Our present knowledge of what happens in the nervous system during development is greatly strained by this bold procedure. In cases such as that of the gray goose, which have been studied only postnatally and, in the adult form, the behavior processes are not necessarily locked within neural centers until the act catches our attention in its adaptive form, (e.g., egg-rolling). We are not in a position to exclude other developmental prerequisites. For all we know at present, the operation of egg-rolling may depend in part upon organism-environment relationships even in earlier post-hatching life, and even in the earlier stages of incubation.

I believe that there are some important differences in the way various workers on behavior, including present company, search for and interpret evidence. Let me emphasize that I am no more favorable to underestimating, and certainly not to ignoring, hereditary factors underlying species-typical behavior than are ethologists affiliated with Prof. Lorenz's theory. But even before I heard about Dr. Lorenz's fascinating work, around 1930 and six years before I read *Der Kumpan*…,[1] I affiliated myself with a less positivistic, less deductive and more inductive point of view dedicated to finding how such factors really influence behavior typically appearing in different species. For taxonomic purposes,

[1] This was a common shorthand among ethologists to refer to Lorenz's 1935 article: "Der Kumpan in der Umwelt des Vogels. Der Artgenosse als auslösendes Moment sozialer Verhaltungsweisen" (The companion in the bird's world. The fellow-member of the species as releasing factor of social behavior) *Journal für Ornithologie. Beiblatt* 83:137–213.

and genetic studies, naturally, expedients such as the IRM or other presumed one-to-one relationships between genes and behavioral items will continue to be postulated. But let us recognize that they are expedients and not necessarily absolutes, indications of fundamental truths. It is possibly this positivistic and seemingly teleological aspect of Prof. Lorenz's writings which has led to the accusation of finalism. It is most encouraging to hear him deny deserving such an accusation.

O. KOEHLER. —1. Preformationist? Isn't "epigentic" equally adequate? It is my honor to occupy Hans Spemann's chair.

2. Why should genes be effective only at the beginning of ontogeny (p. 2, point 1, conclusions p. IX, point 1)? Genes are reduplicators that are uniformly present in every cell nucleus at every developmental stage. The claim of the speaker strictly contradicts the facts of phenogenetics. Every heritable polyphenic factor that affects development at different time points, such as gene A of Ephestia kühniella, proves the contrary.

3. No objections can be made against Kaspar Hauser-style experiments that are conducted correctly. If several Kaspar Hauser organisms each act the same way, this must be based on heritability. Compare also the Kaspar Hausers that turned completely deaf but still sing the complete species-specific melodies.

4. Phylogeny. When I am standing and make a turn to the left, or keep the position of my legs and turn only my trunk 90 degrees to the left, or turn only the right arm or only the head by 90 degrees, turn my bicycle or the snowshoes by 90 degrees, these are all different mechanisms, but they all are my own left turns. This happens likewise in amoebas, *Ucas* [fiddler crab], bears, and monkeys. The tertium comparationis we call "taxis"; we have made good use of this term and still use it today.

5. Page 11, the rat example: however greater sensitivity of the penis; this is why coitus is not learned but remains innate. How could one ever learn such an immensely complex and coordinated behavior. The animal is merely sexualized stronger and consequently mates more frequently.

6. Purposive, page 13. It looks equally "purposive" when the Amoeba verrucosa attacks the thread-shaped *Oscillaria*, when the leukocyte attacks and devours the *Streptococcus*, when in a time lapse image the *Metridium* leans towards its neighbor who had meat placed on its oral disc, or when a baby grasps for the toy. Unfortunately, I have forgotten at what age as a baby I started doing this purposively.

Mrs. SPURWAY-HALDANE. — The technique by which M. Lorenz diagnoses a movement to be what he calls instinctive is precisely the same technique by which ecotypes are distinguished from ecophenes. "Rearing in isolation" means rearing in one kind of experimental garden. M. Schneirla and M. Lehrman are discussing embryological experiments to elucidate the epigenetics of ecotypes. The botanical equivalent of Lorenz's study has no satisfactory name. It was begun by Gaston Bonnier and is today associated with the names of Turesson of Uppsala and Clausen at Berkeley, to mention only senior workers. The antithesis "innate" and "acquired" has not been used for 30 years in many fields of biology.

T. C. SCHNEIRLA. — The first question asked by Mrs. Haldane is answered very differently according to our attitude toward what "complexity" really means in behavior. I believe that to interpret phyletic differences correctly, behavioral complexity (meaning the number of items of any kind), and qualitative make up (meaning how the behavior is organized and what capacities are involved) must be distinguished. Behavior in a lower invertebrate and in a mammal may both be complex in the sense of this distinction, but the mammal's adjustment to the situation may be very superior in organization and in capacities involved. For instance, I found that a particular maze pattern with six blind alleys is learned both by Formica ants and by white rats. Both habits are complex; in fact, that of the ants is more so than that of the rats, but important qualitative differences are indicated in favor of the mammal. The ants cannot transfer their habit appreciably, but in a different situation (e.g., running to nest instead of to food-box) must relearn the main adjustment. Their habit is mainly restricted to the situation of learning, whereas the rats transfer rather freely. Both are complex habits, but insect and mammal have learned very different kinds of adjustments. The rat can run the maze in reverse if necessary, with an appreciable saving, — the ant has only a minimal saving. The point appears to be similar for behavior ordinarily included under the "instinct" problem, when members of different phyla are compared. Our chief problem concerns how behavior develops from a given genetic basis in each animal type; but both complexity and plasticity may have a different and distinctive meaning for each type, as capacities for organizing and modifying behavior differ. How behavior develops is the problem to solve, rather than distinguishing between what is innate and what is acquired. The latter seems as much a pseudo-problem as does nature vs. nurture, and I have tried to suggest how these concepts "innate" and "acquired" can be improved upon in developmental theory.

As concerns the concept of "ecotype", I believe that current advances in genetics stimulated by ecological considerations are consistent with the type of theoretical approach represented in my paper. To understand either genetic isolation of ecotypes, the extrinsic relations of the organism must be considered, both during development and in the functional mature form. The factors underlying isolation as a result of selection are not shown to be restricted neural factors, but somatic, physiological and behavioral factors. Their change under selection pressure seems to demand a close study of extrinsic-intrinsic relationships in ontogeny.

M. KLEIN.—I was extremely interested by Professor Schneirla, but also discouraged, because I realized that while a psychologist can use the facts revealed by biology in constructing their generalizations, the biologist who experiments must rigorously remain in close contact with the facts. Regarding everything that concerns the biological bases of sexual behavior and particularly parturition, we allow ourselves to refer to our report. It relates to experiments that perhaps allow for distinguishing between innate and acquired factors.

T. C. SCHNEIRLA. — We certainly don't consider these questions of basic mammalian behavior settled, Dr. Klein, and of course we are very interested in the meaning of evidence concerning neurohumoral factors. But the relationships of neurohumoral and other organismic factors to behavior are unfortunately very inadequately understood at present, and in any case do not represent mutually exclusive approaches. Further progress seems to demand a greater variety of approaches. We try to be constantly aware of neurohumoral factors in our work, and plan to incorporate specific tests of them at the appropriate stage in our studies. There are ample illustrations of what significant contributions endocrinological studies can make to these problems, and Dr. Klein's own work furnishes some good instances. But it is probable that no one branch of biology can solve the problems of instinctive behavior alone; instead, better coordination of various approaches is called for.

I have tried to show that the dichotomy of the innate and the learned has been carried too far in such studies; so far that it has obscured ontogenetic factors which may prove to be critical. Interactions of organism and developmental context are highly complex and demand analytical study; neither endocrine factors nor any others produce behavior directly. In animals raised apart from their kind, abnormalities in mating are common but are not traceable to specific organic factors, — specific glandular or other physiological deficiencies have not been demonstrated as sole primary factors. And in the "collared rats" in the experiment of Birch, at least one of the important factors underlying maternal failure seems to be habitual and perceptual grounded in the conditions of development. Specific organic factors have not been isolated as causing the results, and the physiological factors indicated may be secondary. Perceptual orientation seems to be among the important intervening variables accounting for the appearance of such patterns, but certainly factors such as endocrine effects must also be considered in the causal pattern of parturition and litter care.

D. LEHRMAN. — It appears that Dr. Lorenz and Dr. Schneirla do not mean quite the same thing when they speak of the analysis of ontogeny. I mean no disrespect for Heinroth's monumental work when I say that his studies of ontogeny were descriptive studies, inventories, of the order of development of various behavior patterns, and interspecific comparisons of them. This is, of course, extremely valuable, but it does not yet throw light on the nature of the processes underlying the development. Indeed, the purely descriptive nature of Heinroth's (and Lorenz's) studies of ontogeny may have facilitated the development of what is, in our opinion, the too-simple idea that the development of each movement pattern reflects the self-differentiation of a motor center specific to it, and which contains the coordination intra-centrally. This is a very early stage of ontogenetic analysis, and physiological assumptions based on the idea of isomorphism between the developing movements and the developing motor centers are likely to be misleading. Just as in the case of experimental embryology, we need an attitude of not being satisfied with formal descriptions of developmental sequences, but of needing insight into the developmental relations and forces which give rise to these sequences. Such an attitude may lead, very often, to the discovery that unlearned behavior patterns depend just as much on the inheritance of peripheral as of central features of the animal. It may clarify matters if I try to disentangle the issues in the case of the immature Bearded Tit's display. No one can claim that this movement pattern must be learned.

But the fact that it appears before the feathers which it displays have grown in does not necessarily mean that it emanates fully-formed from a motor center. Such a conclusion implies knowledge about the histological situation in the musculature of the beard area, and information about the conditions of sensitivity and afferent inflow and receptor distribution there, which we simply do not possess. There are actually very, very few cases where we seem to have enough sound information to make the leap from the fact of autogenous variation in irritability in the CNS to the assumption of the endogenous production of complex behavior patterns. These cases are in lower animals, are about a lower-level coordination (locomotion) and are entangled in conflicting evidence.

Assumptions about what is innate will be on a much more secure basis when we have more information about the physiological genetics of behavior. Isolation experiments give certain information about the non-relevance of some kinds of experience, but do not say anything about where or at what level or at what age the "innateness" lies. We should have (and I hope soon to have for doves) information about correlated genetic and physiological studies of differences in social behavior patterns, as we already have, to some extent, about wildness and tameness in turkeys and rats, or about some differences in temperament in dogs.

Without the physiological-genetic approach, more genetic information will not settle the question of the relationship, for example, between innateness and endogeneity.

Many of these problems are, of course, already inherent in the data made available by ethological research. I wonder, however, whether it may be that the concentration on formal descriptions, on isomorphic assumptions of central nervous function, and on the somewhat artificial dichotomy between innate and acquired, prevents ethological students from being attracted to ontogenetic studies, in the sense used by Schneirla.

T. C. SCHNEIRLA. — This remark of Dr. Lehrman's appropriately brings in a part of my paper which was only mentioned in the talk. The study of Van der Kloot and Williams belongs in such a discussion as an example of a significant analysis of a behavior pattern in a solitary insect. In my ms. the point is made that while this study reveals both endogenous and extrinsic factors underlying the appearance of cocoon-spinning in the Cecropia caterpillar, these must be considered as closely interrelated both in development and in function. In the behavior pattern of spinning, only in an abstract manner can we consider either intrinsic or extrinsic aspects as effective without the other.

And in the vertebrate sphere, when the problem is carried into further detail we find physiological factors such as those discussed by Dr. Benoit most relevant for the understanding of interrelationships between stages in development. I have discussed some of the other functions which seem to implement the ontogenetic progression. It is another aspect of the situation I mentioned in commenting on Prof. Klein's response to my paper.

D. MORRIS. — I would like to thank Prof. Schneirla for all the work he has done in pointing out the dangers involved in some of the conceptual dichotomies employed by ethologists, for example the dualism of innate–acquired. But I think he would agree about the fundamental place which such dichotomies hold in our scientific thinking (innate–acquired, matured learnt, internal–external etc…). Clearly, this is a very convenient way of approaching the basic problems of behaviour, and I feel that much of the criticism that has been levelled against Prof. Schneirla's ideas, has been the result of a feeling that he is denying such dualism. But I do not think that his theorizing is incompatible with certain dichotomies. I agree with him fully that the innate–acquired dualism, as used by ethologists, in the past, has been most unfortunate. It has probably been the cause of more wastage of time and energy than any other concept in behaviour. But I wonder if he would accept that the following dichotomy is not only convenient for our actual researches but also free from the dangers he has discussed.

I suggest that we can consider all behaviour as the result of the effect on the zygote of two types of experience, firstly there is species experience, and secondly there is particular individual experience. Species experience is common to all members of a species, starts from the specific zygote, and proceeds step by step in an inevitable sequence under the conditions natural to that species. (The genetic variation which exists in a species can be overlooked here). (What has preoccupied Schneirla and Lehrman is the effect of such developmental stages on subsequent stages). Then, with special-individual-experience, we are dealing with those effects which operate uniquely in the case of each individual. This dichotomy is near to the maturation–learning one, but, as Schneirla and Lehrman have pointed out, the cloaking of species experience–development under the name of maturation has led to some concealment of the problems of behaviour ontogeny.

I will conclude by giving an example to clarify my point: an animal may develop a red colour or a response to a red colour as the result of a long chain of "species-experience" common to all individuals of that species (except those artificially altered by experimenters), but such an animal may, in one individual, respond to a "black pebble next to a crooked twig" on the border of its territory and such a response will occur only in that individual of the species and is the result of individual-experience. Both types of experience can be analysed and now I come to my disagreement with Schneirla and Lehrman. They seem to think that, because ethologists have cloaked behaviour ontogeny problems under such words as "innate" or "maturation" this has been detrimental not only to the understanding of behaviour ontogeny, but also to the understanding of all other problems of ethology. I agree with the first, but not the second. I do not believe that the studies of such aspects of ethology as behaviour taxonomy, for example, and other non-ontogenetic aspects of behaviour, have suffered much from our attitude to maturation.

T. C. SCHNEIRLA. — I agree in essence with Dr. Morris's point and would add only this. Sometimes a theoretical dichotomy is logically useful in the introductory stages of an investigation but may involve artificial distinctions opposing further advances. I believe the dichotomy of the innate and acquired falls into this class with respect to "instinct" theory, and needs some drastic correction and improvement as I have suggested. Although the concepts of maturation and experience as I have defined them also involve a dichotomy, in keeping with scientific progress it is a less rigid one representing overlapping, fused, closely interrelated systems in ontogeny. One important improvement is a stronger and somewhat different emphasis upon interrelationships through development and upon the role of trace effects; another is an emphasis upon factors of early experience, feedback and extrinsic factors and the trace effects of these, antedating learning if the species has this capacity.

To repeat, I think it is crucial whether the members of a dichotomy are treated as mutually exclusive and sharply separable or as capable of entering into different classes of relationships dependent on their context.

E. PH. DELEURANCE. — I would like to make a few remarks on Professor Schneirla's presentation:

1. He states, "In certain species of *Formica* ants for example, a habituation to the colony odor may begin in the larval stage and transfer to some extent to influence a continuation in the adult stage." We know of some cases of such a phenomenon (e.g., Thorpe's experiments on what he calls "larval imprintings"). But this is not general. Thus, in the *Polistes* wasps, I was able to raise a brood of *P. omissus* with subjects of *P. gallicu*s. However, at the birth of the imagos, I noted a total intolerance between the subjects of the two species! In fact, in the *Polistes*, the habituation to the odor of the nest is acquired in the *imaginal* state:

a. If we isolate the imago from birth, we notice that it is generally no longer tolerated by its society after a few days.

b. During the first day after birth, the imago is accepted *on any nest* (we use this characteristic in our experiments on the variations of the imaginal population in the presence of a given brood).

Professor Schneirla's opinion thus seems to me to be at variance with observation. It should be noted that the problem is complex, because it happens that a wasp is absent from the nest for one or even two weeks, and that on its return, it is perfectly tolerated!

2. It seems to me undeniable that trophallaxis plays a very important role in social behavior, especially in insects with complex societies (termites and ants for example). However, in Professor Schneirla's way of conceiving its role on behavior, I note that it is generally an action limited to the *initiation* of an activity. It does not seem to me to be demonstrated that it has a role in *creating* behavior. The activity of insects seems to me to be very stereotyped, and the part of the acquired, always weak, does not seem to me to hold a *fundamental* role there.

Let us note in passing the extreme difficulty that there would be in interpreting from this point of view the very complex reproductive behavior of many predatory hymenopterans! To conceive it as acquired seems to me impossible.

3. I agree entirely with Professor Schneirla on the fundamental action of organic factors. He has demonstrated this in his admirable work on *Eciton* ants: it is a major step forward in our knowledge of the behavior of insect societies. The role of organic factors is at the base of the general evolution of insect societies. Thus, in *Polistes* (I will have the occasion to speak to you about it) these factors seem to me to determine the evolution, by successive cycles, of the nest; in the wasp, the fundamental phenomenon would be different from that of *Eciton*: it would relate to the nutritive oophagy (at least for the first cycle).

But, these organic factors seem to me to act on the organization and the intensity of stereotyped behaviors (like harvesting, building, etc…), *which, themselves, do not seem to depend on learning*. The observer cannot avoid the idea that they are fundamentally preexisting and that they do not belong to the phenomena that we usually consider as belonging to acquired behavior (i.e., plastic).

One can argue about the meaning of the word "innate", but one can hardly include under the same term "learning" phenomena such as the conditioning in the larval state, for example, of a factor which will reappear in the adult state (cf. also Dr. Lehrman, the case of the turtledoves which have a preferential copulation with the species which raised them in their young age). Pavlov, in his book on conditioned reflexes, insists on the necessity of "maintaining" the conditioning in order to maintain the acquired "habit". I don't think he would have agreed with such an extension of his notion of the conditioned reflex. In conditioning, we study the action of immediate factors on behavior. In the ontogeny of behavior, as outlined by Professor Schneirla, we are dealing with much more complex phenomena. Conditioning may play a role (I believe it does!) but how many more phenomena are there not?

I think it would be appropriate to clearly define what the author means by "behaviour pattern".

M. SCHNEIRLA. — Here and now I can offer no clear hypothesis for the spontaneous social reactions which Dr. Deleurance has demonstrated in his wasps. As with many other types of spontaneous reactions in insects and other animals, more should be known about ontogenetic background before we can say what is essential to their appearance. Experimental change of the developmental situation may be enlightening.

On the other hand, various lines of evidence suggest that situational effects may be important in the behavioral development of numerous social insects and others. The effect of pervasive colony odor on the later social reactions of the newly emerged callow ant is a case which we understand only partially. The circumstances of such effects may differ greatly for species, according to their organic makeup as concerns glandular factors, for example.

That is, an isolated insect has developed the species-typical glands, and thereby can stimulate itself variously in species-typical ways. This is only one of numerous possibilities. Experiments involving nest-environment changes in larval cf. pupal stages should be worthwhile. Early habituation is one possible factor, and such factors must be expected to apply to different species and eco-races in different ways and to different extents. This for one seems worth testing in very different contexts, in relation to the progressive function of feeding reflexes, for example, the appearance of foraging, and the like.

A concept only partially clarified and explored is "trophallaxis", exchange-of-stimulation as a factor in the rise of group organization. Granted that its role is more limited in some cases than others, this very fact is a significant lead to the analysis of species social patterns and their development. A great variety of organism-environment interactions is indicated, and many types of individual stimulative relationships. For example, in the appearance of such behavior, what is the influence of species-typical equipment promoting regurgitation, in some social insects, or the influence of tufts of hairs associated with secretory tissues (as in certain inquilines)? Comparative study of such matters has scarcely begun. Each such piece of morphological equipment should be regarded as a part of the context in which the given behavior develops, influential not only intrinsically but also an interacting with and contributing to the prevailing extrinsic situation.

The nest is another complex of factors which must be analyzed for each insect type. I have suggested its role in the appearance and maintenance of species functional patterns in army ants. But this factor is not produced simply through predetermined endogenous organizations, — rather it results from complex interrelationships of factors from many sources: those concerning different types of individuals interacting with one another and with the extrinsic setting.

M. HALDANE—In this Colloquium, we come up against linguistic difficulties. Now, quite often an Englishman understands French, German, Italian, perhaps even Russian, better than American English, and no doubt Americans have similar difficulties. If, therefore, I have understood Mr. Schneirla and Mr. Lehrman correctly, I address to them the following criticisms:

1. I light this paper. I say it burns because I lit it. Mr. Schneirla may say that I am wrong because the paper would not burn if we were in a vacuum or in nitrogen. I say that the difference between a lit paper and an unlit paper is a matter of matches and not of oxygen. I also say that the difference in behavior between a young sparrow and a young duck depends on genotype, not experience.

Any character of an adult organism is a character acquired during its ontogeny. This does not mean that it is not an innate trait. Innate morphological characters are quite often acquired by those intercellular trophallaxis which are called hormonal action and induction. It is a major goal of modern genetics to make causal analysis of the development of any morphological trait. The success of such analyses will not contradict the fundamental concepts of genetics.

3. Geneticists do not use the word "innate" much. Here is how Darwin used the word.

"The passion for collecting which leads a man to be a systematic naturalist, a virtuoso, or a miser, was very strong in me, and was clearly innate, as none of my sisters or brother ever had this taste". (*Autobiography*, p. 3)

4. Let's cross out, if you agree, the noun "instinct", but not the adjective "instinctive". But let's also cross out the word "learning", which is much less clear. As for me, I prefer to keep the word "instinctive" for behaviors as stable as morphological traits.

M. SCHNEIRLA. — Prof. Haldane's match-and-paper illustration serves nicely up to a point. It seems to suggest fairly well many of the endogenous-extrinsic interrelationships which 1 have discussed for the development of instinctive behavior. Of course to predict the result we must consider not only kind of paper but also how it has been prepared for the test, also the match, atmospheric conditions, and so on. As Prof. Haldane's own writings bring out, to follow this analogy, certain types of paper burn more readily than others under most conditions, but certain conditions favor burning in all papers. To understand these differences, paper burning must be represented as a chemical reaction, in which differences both in "paper genetics" and "paper experience" and their varieties of possible interrelationships come into play.

I think that geneticists themselves have contributed considerably to the point of view represented in my paper. Thus the word "innate" is not often used by geneticists in their theory, because (it would seem) of an awareness that while species-typical patterns basically concern the different genotypes, these are expressed only through a multitude of extrinsic circumstances necessarily bound up in the developmental processes of the species.

I am not suggesting that the concept "instinct" be crossed out from the list merely because it encourages overlooking the complexity of the intervening variables and often encourages accepting a one-to-one relationship between genes and behavior. But I prefer "instinctive" behavior as a lesser evil, since it is still recognized that the contribution of the genotype is basic to species typical behavior, however indirectly genes are related to phenotype. In my treatment of the concept of "maturation" I have suggested concentrating upon the study of variations in species development under different conditions, — focussing upon the nature of developmental interrelationships rather than upon hereditary background or upon extrinsic influences as though either could be regarded as unitary. No more, it should be added, can the concept "learning" be used as though it referred to separable and distinct processes in development. Z. Y. Kuo, one of those who argued vehemently for giving up "instinct", also favored giving up "learning" for similar reasons. The point is not to hamstring ourselves by discarding useful concepts, but to improve them by relating them better to reality. I think the concepts of "maturation" and "experience" better express the real picture of relationships in ontogeny than innate and acquired.

M. SCHNEIRLA [to] M. LORENZ. — Certainly this series of graduated behavior patterns in related species is important material for behavioral analysis. But we find them in all parts of the animal series, and it does not seem likely that one theoretical formula will account for them all, — at least until striking differences in capacity and organization are taken into account. Correspondences can be described between species morphological characteristics and typical aspects of species behavior, but the connection is not necessarily the same in different phyla. The characteristic movements, stereotyped movements, "instinctive movements" and the like, may have very different relationships to the context of development on the various phyletic levels. In my discussion of the concepts of maturation and experience I tried to bring out some of the possibilities.

An important problem of this kind, which I could only mention, is the problem of isolation mechanisms in speciation. Here cases have been reported in which one specific factor of morphology or of behavior seems responsible for the isolation, a true lock-and-key relationship opposing crossing of species. But good studies are few, and for the case of certain xiphophorin fishes Clark, Aronson and Gordon negate this simple interpretation. They find instead that the isolation mechanism concerns factors of many kinds in morphology, physiology and behavior, complexly interrelated, and with an involved genetic background. It would appear that emphasis upon the most apparent morphological–behavioral correspondences as presumed lock-and-key devices may not only oversimplify the ontogenetic processes accounting for behavior patterns, but actually misrepresent them. And there is reason to expect that their genetic bases may also be comparably misrepresented.

Acknowledgments G.K. and the journal's editors would like to thank the discussion translators for their generous assistance and carefully crafted renderings: Gerd B. Müller of the University of Vienna and KLI Klosterneuburg, Austria, who translated the German passages; and Mathieu Charbonneau of the University Mohammed VI Polytechnic, Morocco, who translated the French.

Funding No funding was received to assist with the preparation of this article.

Availability of data and materials Every reasonable effort has been made to supply complete and correct credits; if there are errors or omissions, please contact Springer Nature so that corrections can be addressed in any subsequent publication.

Declarations

Competing Interests The author has no relevant conflicts of interest to declare.

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