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Revisiting T. C. Schneirla's "Interrelationships of the 'Innate' and the 'Acquired' in Instinctive Behavior" (1956)

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Abstract

During the postwar period, the concept of instinct came to encapsulate the debate around the importance of nature versus nurture. The fact that animals show highly organized behavior early in development suggested the presence of an underlying fixity where behavior was "inbuilt" into an animal's biology despite an individual's experiences. This placed a discrete and exhaustive line between the innate and acquired that became a foundation for the European-dominated field of ethology. Across the Atlantic, a group of comparative psychologists led by the American Museum of Natural History's T. C. Schneirla contested this approach, proposing that the study of animal behavior should avoid abstract dichotomies with a renewed focus on developmental processes. While Schneirla's theoretical and empirical work shaped the modern study of animal behavior, his legacy requires revisiting in an era where the nature versus nurture debate is regaining prominence. In this article, I revisit Schneirla's approach to behavior with a focus on his paper "Interrelationships of the 'Innate' and the 'Acquired' in Instinctive Behavior" (published in M. Autuori et al. (1956) *L'instinct dans le comportement des animaux et de l'homme*; Masson, Paris, pp. 387–452) for the journal's "Classics in Biological Theory" collection; the paper is available as supplementary material in the online version of this article. A companion article (this issue; G. M. Kohn (2024) "A Discussion on Instinct, Paris, 1954") presents the commentary that was published with it.

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Introduction: The Emergence of the Innate and the Acquired in Animal Behavior

During the late 1800s, a young lawyer, laborer, and tutor named Douglas A. Spalding conducted a series of experiments that would change the study of animal behavior. Before Spalding, the study of instincts—fixed patterns of behavior characteristic of a specific species—was largely descriptive and observational. Spalding, however, was unsatisfied with descriptive accounts and developed methods specifically aimed at uncovering instinctive behaviors (Spalding 1875). By isolating young individuals from certain experiences during early life, Spalding claimed we could objectively separate the "instinctual" from the "acquired." This transformed the study of instincts from an observational science to an experimental one, as he was among the first researchers to experimentally control the types of experiences an organism had and show the influence of this control on its behavioral development (Gray 1962).

The methods pioneered by Spalding laid the foundation for the modern concept of innateness. He raised swallows in small boxes without the room to stretch their wings and blindfolded newly hatched chicks to remove the influence of light. He found that such manipulations often did little to hamper the animals' faculties, as swallows flew shortly after being released from their box, and the newly unblindfolded chicks readily tracked and pecked at moving objects. Such results suggested a strong line separating the innate and the acquired, a line that is still central to many who research the development of behavior (Vallortigara 2021). It also set the modern boundaries for what was considered innate, where innate behaviors were organized responses that developed independently from individuals' prior experiences.

The innate–acquired separation assumes that some behaviors are so essential to the existence of an organism that they are built into the organism's biological architecture

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from the beginning of life. Since no specific experience is necessary or sufficient to cause these behaviors, and as long as an individual is healthy, they will have them. Working within this paradigm, researchers aim to uncover which behaviors depend on an individual's experiences, and which do not. To do this would require not just removing a specific experience, or even a range of experiences, but removing the ability of an organism to experience its environment at all.

In the 1920s a young researcher named Leonard Carmichael did just that, and attempted to go beyond Spalding's isolation tests and completely remove an individual's ability to experience its environment. In these experiments, Carmichael applied chloretone to salamander embryos. This blocked the ability of the embryo to move during development, thus severely limiting its ability to experience its prenatal environment. Nonetheless, after the young had developed into adults the effects of the drug were removed, and they swam in a supposedly identical fashion to undrugged controls (Carmichael 1926, 1927).

During this period a new science of animal behavior was emerging in North America and Europe. This science was called ethology, and it proposed that the behavior of animals should be investigated from an evolutionary perspective. The early ethologists maintained that behavior could be seen as an extension of morphology, something that had been intricately shaped by natural selection, and that by comparing the structure of behavior across species we would gain insights into how and why it evolved. In North America, Charles Otis Whitman spent significant efforts to describe and compare the behavior of pigeon species in his home laboratory, while in the Berlin Aquarium, Oskar Heinroth developed techniques to measure the stereotypical behavior patterns shown in Anatidae (Heinroth 1911; Whitman 1919; Podos 1994). These studies provided the foundation for the careers of Konrad Lorenz and Niko Tinbergen, today recognized as the founders of modern ethology. The advances made by Lorenz and Tinbergen were to ground behavioral comparisons across species within the concept of innateness.

Fig. 1 Photograph of T. C. Schneirla, 1952 (photo by United Press)

Carmichael's study became an inspiration for the budding science of ethology. During this period taxonomists used morphological traits as the unit of comparison between species. If two species shared similar morphologies, it suggested they also shared a close evolutionary ancestor. However, unlike morphology, behavior is dynamic, and learning meant that behavioral similarities across species could be caused by similar experiences rather than shared evolutionary ancestry. The early ethologists sought to find an equivalent unit with which to compare behavior across species, and innate traits provided an opening.

Innate behaviors have the necessary qualities to be useful in species comparisons. Firstly, their supposed independence from experience meant the behavior should have a discrete identifiable structure across individuals of the same species. Secondly, the expression of the behavior even under the most austere rearing conditions suggested the behavior was genetically determined, and thus a reflection of past selective pressures. These two assumptions became fundamental to how early ethologists investigated the evolution of behavioral abilities. They motivated the work of both Lorenz (1937) and Tinbergen (2020) who emphasized Carmichael's studies when they proposed that studying behavioral evolution requires the identification and comparison of instincts. The role of experiences in the evolution of instinctive behavior was regarded as superfluous, distracting, or even outright incorrect.

Reintroducing T. C. Schneirla

The notion of the strong separation between the innate and the acquired motivated the science of animal behavior until the postwar period, but it was not universally accepted among all researchers in animal behavior. Among its most vociferous critics was a comparative psychologist named Theodore Christian Schneirla (1902–1968; Fig. 1). The "classic" paper featured in this introduction is Schneirla's "Interrelationships of the 'Innate' and the 'Acquired' in Instinctive Behavior," which was originally published in the book *L'instinct dans le comportement des animaux et de l'homme* (Schneirla 1956). The book is a compendium of different perspectives on the concept of instinct drawn from a symposium held in 1954 in France. While previous papers by Schneirla often touched upon the problems associated with the innate–acquired dichotomy, the 1956 paper featured here was the first to outline a detailed and comprehensive critique of it.

Schneirla was not the typical comparative psychologist—he was more likely to be found collecting ants in the rainforests of Panama than operating a Skinner box in a windowless lab. During his career, Schneirla spearheaded a unique and truly comparative approach to studying animal behavior that was rooted in biology, psychology, and natural history. Over time, aspects of Schneirla's perspective were absorbed into the then-nascent sciences of animal behavior and developmental psychobiology, and his influence can still be found in developmental psychology, neuroscience, and even artificial intelligence and robotics today.

Schneirla was born to celery farmers in Michigan on July 23, 1907. He earned his PhD under the supervision of Dr. John F. Shepard at the University of Michigan. While Shepard's primary interest was maze learning, he was also interested in the development of instinctual behavior. In 1913 Shepard and F. S. Breed published "Maturation and Use in the Development of an Instinct" (Shepard and Breed 1913) where they investigated the development of pecking behaviors in chicks. In this paper they critiqued the isolation methods employed by Spalding, highlighting the multiple routes in which experiences may have shaped the chick's behavior. While it's unknown if Shepard's critique of instincts made an impact on the young Schneirla, he often mentioned that his studies during graduate school were motivated by questions "concerning species biological makeup as related to species behavior pattern" (Maier and Schneirla 1964, p. 68).

After finishing his PhD, he started teaching at New York University but also spent time working in Karl Lashley's laboratory at the University of Chicago. While in Lashley's lab, Schneirla befriended Norman and Ayesha Maier. His association with Norman Maier lead to the publication of *Principles of Animal Psychology* in 1935 (Maier and Schneirla 1964). This book was one of the first comprehensive textbooks to cover comparative psychology, remaining in print until the 1970s and providing a theoretical foundation for this new field. This novel approach was distinct from the behaviorism of the time that focused on universal laws of learning unconstrained by biological differences across species. Instead, Schneirla and Maier's book focused on understanding differences in the behavioral abilities across species, the emergence of different levels of behavioral organization across phyla, and the motivational principles governing the development of behavior. The book was exceptional in the diversity of behavior it covered, ranging from the phototropic behavior of plants, and the movement of protists, to the use of planning and forethought in chimpanzees.

The breadth and theoretical foundations outlined in the *Principles of Animal Psychology* provided the seed for the development of empirical and theoretical advances in comparative psychology. One particular advance was its focus on the development of species-typical behavior. While an organism's sensory organs shape how it specifically perceives the world, Schneirla noted that during early development behavioral responses were generally tuned to the intensity of stimulation from the environment. A large and sudden onset of sensory input was often followed by a withdrawal-related response, where moderate to light onsets of sensory input were met with an approach-related response. This theory of approach-withdrawal maintained that the study of species-typical behaviors should be rooted in the refinement of these general approach-withdrawal responses over development, wherein unspecified responses to stimulus intensity become tailored to specific behaviors to specific inputs.

After the publication of *Principles of Animal Psychology*, Schneirla's research shifted from a focus on ant maze learning to the development and organization of social structure. In 1932 Schneirla made his first trip to Barro Colorado Island in Panama to study the social organization and mechanisms of colony formation in two species of doryline army ants. This started a career-long occupation that bounced between the field and the lab, to uncover how interactions between colony composition, individual development, and ecological context shaped species-typical patterns of social organization. Along the way, this research also contributed to his critique of the innate–acquired dichotomy. In 1943 Schneirla was asked to join the American Museum of Natural History in New York by its director Frank Beach, eventually becoming a curator in the animal behavior department in 1945. During this period Schneirla undertook many different expeditions across the southern United States, Mexico, Thailand, and the Philippines to study the social organization of different ant species, and built up the Department of Animal Behavior at the Museum.

The publication of "Interrelationships of the 'Innate' and the 'Acquired' in Instinctive Behavior" in 1956 occurred at a critical crossroads for the study of animal behavior. Researchers on both sides of the Atlantic were reflecting on how the study of animal behavior related to the larger geopolitical issues that had unfolded in the previous decades. In 1942 and 1944 the Austrian ethologist Konrad Lorenz published the papers "Die angeborenen Formen moghcher Erfahrungen" and "Durch Domestikation verursachte Storungen." In these papers, Lorenz used the structure of seemingly innate behaviors in waterfowl to argue against the interbreeding of human races (Klopfer 1994). One of the ideas that most resonated with the ruling Nazi regime was the concept of instinct: that individuals possessed a series of fixed behavioral abilities by being a member of a particular species or population.

The ensuing debate around the origins of instincts in ethology came to encapsulate the debate between innate versus acquired abilities. This debate came to a head with the publication of "A Critique of Konrad Lorenz's Theory of Instinctive Behavior" by Schneirla's doctoral student Daniel Lehrman (Lehrman 1953). In this paper, Lehrman showed that methods used to justify the innateness of behavior often fell short of controlling for all causal experiences, and that common techniques used to identify innate behavior, such as isolating individuals, simply removed a subset of potential experiences but did not discount that the behaviors were in some fashion "acquired" through interactions with the environment.

The fallout from Lehrman's paper spread throughout the study of animal behavior. A friendship developed between Lehrman and Tinbergen that eventually led to a reconciliation between comparative psychology and ethology. Tinbergen distanced himself from using the term innate and even called it "heuristically harmful" in his classic 1963 paper, "On the Aims and Methods of Ethology" (Tinbergen 1963). Leading ethologists such as Robert Hinde, Patrick Bateson, and Johan Bolhuis attempted to reorient the field by integrating developmental perspectives. Meanwhile, developmental psychobiologists such as Gilbert Gottlieb, Zing-Yang Kuo, and Sergei Khayutin used the ideas put forward by Schneirla to investigate the development of species-typical abilities (Kuo 1967; Khayutin and Dmitrieva 1981; Gottlieb 2014). With the publication of the textbook *Animal Behavior: Synthesis of Ethology and Comparative Psychology* by Robert Hinde it seemed for a moment as if animal behavior was finally moving beyond the innate–acquired dichotomy (Hinde 1966).

Schneirla died in 1968, just before a revitalization of the support of innateness began in the behavioral sciences. While Lorenz initially softened his view on innateness, he returned to a strong commitment to the innate–acquired dichotomy in his 1965 book *Modification and Evolution of Behavior*. In 1975, E. O. Wilson published *Sociobiology* which called for a new science of behavior centered on investigating the adaptive function of behavior (Wilson 2000). He proposed that adaptive behaviors were largely instinctual and borrowed Lorenzian conceptions of innateness to support these assumptions. Wilson (2000, p. 22) stated that Lorenz "convinced us that behavior and social structure, like all other biological phenomena, can be studied as 'organs,' extensions of the genes that exist because of their superior adaptive value."

While sociobiology came to dominate the study of animal behavior, the use of innateness was also expanding in other fields. Linguist Noam Chomsky's 1967 response to radical behaviorism proposed that the environment was too "information poor" to cause the sophisticated abilities seen in human language, and thus language must rely on innate cognitive devices (Chomsky 1959). Within behavioral neuroscience, many research programs aim to discover the innate circuity underpinning behaviors through the use of isolation techniques (Barabási et al. 2022). In artificial intelligence, some advocate mimicking the supposed innate programs in animals to increase the performance of artificial neural networks (Kohn and Kostecki 2022). Innateness is back on the menu again (Zador 2019).

With this revival of innateness in our purview, now may be an especially important time to revisit the ideas of Schneirla. While Lehrman's paper is credited with shifting the tides against the innate–acquired dichotomy in animal behavior, it was built on a theoretical tradition first championed by Schneirla. Lehrman states that, "if I were going to name a person in the field who had a main effect of giving me a theoretical orientation it would be T. C. Schneirla" (Beer et al. 1986, p. xiii). Schneirla's 1956 paper encapsulated his critique of innateness by highlighting the theoretical and empirical limits of the concept from the perspective of a developmentalist. But at its core, Schneirla's critique also proposes a new way to envision the role of experience in development: one where an animal's experiences no longer simply passively support innate biological mechanisms, but become necessary and critical components in organizing those mechanisms.

Constructive Experiences and Development

The idea that fixed biological structures emerge regardless of specific experiences is central to innateness. It's supposed that some biological structures are so essential to survival that as long as an organism is alive, these structures will develop. Nonetheless, organisms require experiences merely to live, as any organisms denied access to food, water, or other necessities will quickly perish. Therefore, to maintain the notion of innateness, experiences are often divided into two broad categories: supportive and constructive ones.

A supportive experience is necessary for the animal to live, but doesn't specifically shape, cause, guide, or influence the emergence of behavior. Imagine a computer sitting on a desk in a typical office. Desks, outlets, and the wider office room represent supportive experiences. For the computer to function it requires an outlet for electricity, a desk so a person can interact with it, and a room to protect it from the outdoors. While all of these "experiences" are necessary, none will ever structure the "behavior" of the computer. The computer's behavior depends in large part on the programs installed on it. Upon entering the room no experience will program a piece of software, and no amount of input from the electrical outlet, desk, or room will write a line of code for the operating system. From the perspective of the consumer these features are innate, they simply await the right supportive environment to become activated.

While organisms aren't computers, many have assumed that similar programs exist in the organism's genes. The metaphor of the innate program is a common device to describe the way that genes shape developmental processes through the storage and expression of information. For innate programs to run, the role of experience is solely to turn on the genetic program and release the information stored within it. As such, experiences are assumed to only be supportive; the program itself is an inbuilt, fixed, and inherited characteristic of the species genome whether it is expressed or not.

Schneirla challenged this notion and emphasized that to truly understand species-typical behaviors we need to emphasize constructive experiences. While the term "constructive" was not used in his 1956 paper, this paper was pivotal in spearheading the concept in the then-nascent field of developmental psychobiology. A constructive experience is one that specifically contributes to the structure of behavior over development. He proposed that experiencing one's "environment does not merely elicit pre-organized mechanisms of behavioral adjustment, but is itself implicated in the development of such mechanisms" (Schneirla 1956, p. 417). Using the computer analogy above, a constructive experience would be uploading a specific line of code to a computer so it "behaves" in a specific fashion. These experiences *construct* the behavior, and without them, the behavior doesn't develop in its observed form even if the specific experience is unnecessary to the general functioning of the organism.

The aim of centering the study of development on constructive experiences was not to diminish the importance of other factors but to better understand the causal role they play in development. Schneirla treated genes and neural circuits as components that were necessary, but not sufficient, to understand behavioral development. This breaks with many conventions and dichotomies that continue to define the science of behavior. The idea that the winding probabilistic road from gene to behavior can be gleaned through the removal of experiences receives a lot of criticism in the featured paper, and in writings of Schneirla's students. As stated in the paper:

> appearance in isolation, however sound at first sight, rests too heavily upon an incomplete understanding of equivalence between environments. Even universality is questionable, first of all because of acts that normally are likely to be learned widely throughout a species (Smith and Guthrie 1921). Actually there seem to be no hard and fast rules for distinguishing hypothetically innate behavior from other kinds. (Schneirla 1956, p. 389)

Even today isolation tests are still used in the pursuit of separating the innate from the acquired. Methods such as twin studies and common garden experiments have their roots in isolation tests and assume a priori what range of experiences could play a constructive role. For example, in behavioral genetics, the equal environment assumption assumes that monozygotic and dizygotic twins experience the same environment if they were raised in the same household. Behavioral neuroscience studies raise anesthetized zebrafish embryos to discover innate neural circuity and behavior using methods akin to Carmichael's classic study. Such approaches do not attempt to measure which experiences an individual has but assume that any confounding constructive experiences obscuring an innate structure were removed. In summary, many of the isolation methods critiqued by Schneirla and Lehrman still inform the work of those interested in separating the innate from the acquired.

While isolation methods identify what experiences are *not* necessary, they struggle to identify which experiences *are* necessary. During isolation, the mechanisms causing the behavior are still unknown, and in practice, if behavior is universal (or species-typical) and appears in isolation, it is still commonly treated as innate and under direct genetic control. The mere existence of well-formed responses during early life does not itself reveal any insights into which experiences are necessary. Even in isolation, aspects of the environment persist that could play a directly constructive role in the emergence of behavior. From conception onwards, an organism is immersed in the influence of its environment, and the position advocated by Schneirla seeks to understand what aspects of this influence *are* essential for the construction of behavior.

Constructive experiences aren't something that exist alongside genetic programs—their existence at the beginning of ontogeny challenges the notion that genes contain programs for development. Studies in developmental biology have shown that the "information" for development is a joint product of genes and environmental experiences. Genes are never naked and require organismal systems (cells, tissues, organs, whole organisms) to function. These organismal systems flexibly incorporate both genetic endowments and environmental resources to build themselves over development—it's not just the genes you have, but how you use them that matters (Tung and Levin 2020). Throughout the featured paper we see an effort to shift the study of behavior away from assumptions of genetic control, to a direct investigation of the mechanisms of development, mechanisms which—due to the interactive nature of biological development—contain constructive experiences.

Nonetheless, the emphasis on constructive experiences in development has been controversial. To many researchers, constructive experiences are synonymous with learning, and thus emphasizing them means reducing all development to the mechanisms of learning. In a letter to Anthony Storr, Niko Tinbergen recounts the reaction he received from Konrad Lorenz when he voiced agreement with Schneirla's perspective (Kruuk 2003, p. 301). He wrote: "I agree with Schneirla that we must look at the entire developmental process; Konrad writes to me that it would have been more honest if I had said that I agree with S. that 'everything is learned.' This reading an entirely different meaning into my words is what disturbs me."

Schneirla and other comparative psychologists such as Kuo were keen to emphasize a broader role for experiences beyond learning. While learning requires an organism to form associations between stimuli, experiences can constrain, facilitate, and structure behavioral development outside of associations. For example, the 1956 paper highlights many studies where seemingly innate behaviors expressed at, or directly after, birth have their origins in the constraining influence of the prenatal environment. Ubiquitous factors such as the curvature of the egg or the position of the yolk constrain embryo movements in ways that eventually lead to walking, swallowing, and pecking directly after birth (Kuo 1932a, b, 1967).

Constructive experiences can even arise from experiencing your own body. Schneirla references these self-stimulating aspects of an organism and their role in canalizing species-typical abilities. He proposes that such self-stimulative experiences provide the necessary feedback to calibrate brain-body systems and structure the neural circuitry necessary for later behaviors. Such suggestions predicted many of the findings by Gottlieb and others (Spencer et al. 2009; Gottlieb 2014) which showed that patterns of prenatal self-stimulation are necessary for the development of basic species-typical abilities. For instance, mallard ducklings (*Anas platyrhynchos*) were shown to require the experience of hearing their own vocalizations to later successfully follow maternal contact calls right after leaving the nest; in rats, experiencing their body twitching during sleep calibrates aspects for the motor cortex necessary for later behaviors (Gottlieb 2014; Dooley and Blumberg 2018).

Due to the broad range of constructive experiences, Schneirla and his students argued that we have no a priori knowledge regarding which experiences will be constructive and which won't. As such, he advocated for an inductive approach to behavior wherein "each animal form [is studied] in its own terms as a necessary basis for any comparisons" (Schneirla 1943, p. 235). He was skeptical of the use of metaphors, analogies, and abstractions to motivate research, and wrote that analogies often came at the "expense of analysis," and the use of metaphors serves to "furnish a veneer of ignorance" by becoming explanations in themselves (Schneirla 1943). That the "principles of behavioral organization are not to be satisfied by a priori postulations of innate organizing centers but must be worked out in investigations appropriate to each type of behavior" (Schneirla 1956, p. 406) became a cornerstone of Schneirla's comparative psychology.

However, the call for researchers to investigate behavioral development as directly as possible created an open playing field. What does it mean to investigate an animal on "its own terms"? Without an analogy, metaphor, or a priori postulation to guide one's observation, where does one start an investigation? What was needed was a theoretical foundation to study development. While theories of development remain elusive even today, the 1956 paper laid the ground for such a theory, one centered on the dialectical relationship between experiences and biological changes (Tobach and Greenberg 1984).

An organism's biology is shaped via its experiences with the environment, while at the same time, its biology shapes how it experiences that environment. Behavior is thus a blending of experience and biology over ontogeny, such that understanding one in isolation from the other gives a limited picture. The boundary between the organism and its environment (be it the skin or cell membrane) creates the existence of distinct internal and extrinsic processes. *Maturation* is defined as processes that occur "under the skin," such as tissue differentiation, growth, and organogenesis, while *experiences* are processes that emanate outside of one's skin. The innate–acquired dichotomy assumes independence of some internal and extrinsic processes, but Schneirla aimed to replace this with a maturation–experience dialectic that stressed the dependence on these factors. As he stated:

> The effects of maturation and experience tend to overlap and become integrated through their interactions and organic trace effects. These concepts involve fewer trammeling theoretical assumptions than do "innate" and "acquired", and should replace the latter in theoretical usage. (Schneirla 1956, p. 430)

The maturation–experience approach allows a researcher to investigate development prospectively. Isolation techniques are retroactive: the investigator starts with a well-formed behavior of interest (usually in adulthood) and attempts to control for confounding experiences that occurred in the past. A prospective investigation starts at the earliest period possible and describes the early experiences a young organism has and determines which of those experiences are necessary for future behavioral abilities.

Schneirla describes several prospective research programs throughout the paper, but the work of Zing-Yang Kuo provides a canonical example. Kuo was an important member of the "anti-instinct movement" in the 1920s which advocated for a more inductive approach similar to the one advanced by Schneirla. Throughout his career, Kuo focused on investigating development "from the ground up" by focusing on the early causal prerequisites for behaviors almost universally considered innate. His research relied on firm descriptions of early behavior, and he became a founder of the field of behavioral embryology. For instance, rather than assuming that the pecking and walking behavior of newly hatched chicks was innate, Kuo spent significant effort describing the behavior of embryos, showing how early behaviors and constraints in the egg prefigured post-hatching walking and pecking. The result of this was a research program that uncovered the emergence of walking and pecking while avoiding the use of unobserved variables such as innate programs.

The ultimate aim of a prospective research program in behavioral development is to map its "causal nexus." This nexus reflects how early relationships between an organism and its environment at time *t* cause behavior to develop at time *t* + *1*, which then feeds back into influencing the organism–environmental relationships at time *t* + *2*. By looking forward from time *t* to time *t* + *2* a map of the specific antecedent–consequent relationships that ultimately cause a specific behavior could be identified. As Schneirla (1956, p. 431) stated, these "'feedback' relationships involving interactions between the progressing system, its component processes, and its 'output', frequently play an essential role in the rise of integration and advances from stage to stage."

An illustration of a causal nexus can be seen in Fig. 2. After Schneirla visited Barro Colorado his research shifted to understanding the development of the social organization across different ant species. While a focus on social organization in ants seems distant from the broader conceptual issues surrounding the innate–acquired dichotomy, Schneirla's approach to studying complex ant colonies highlighted the need to look prospectively.

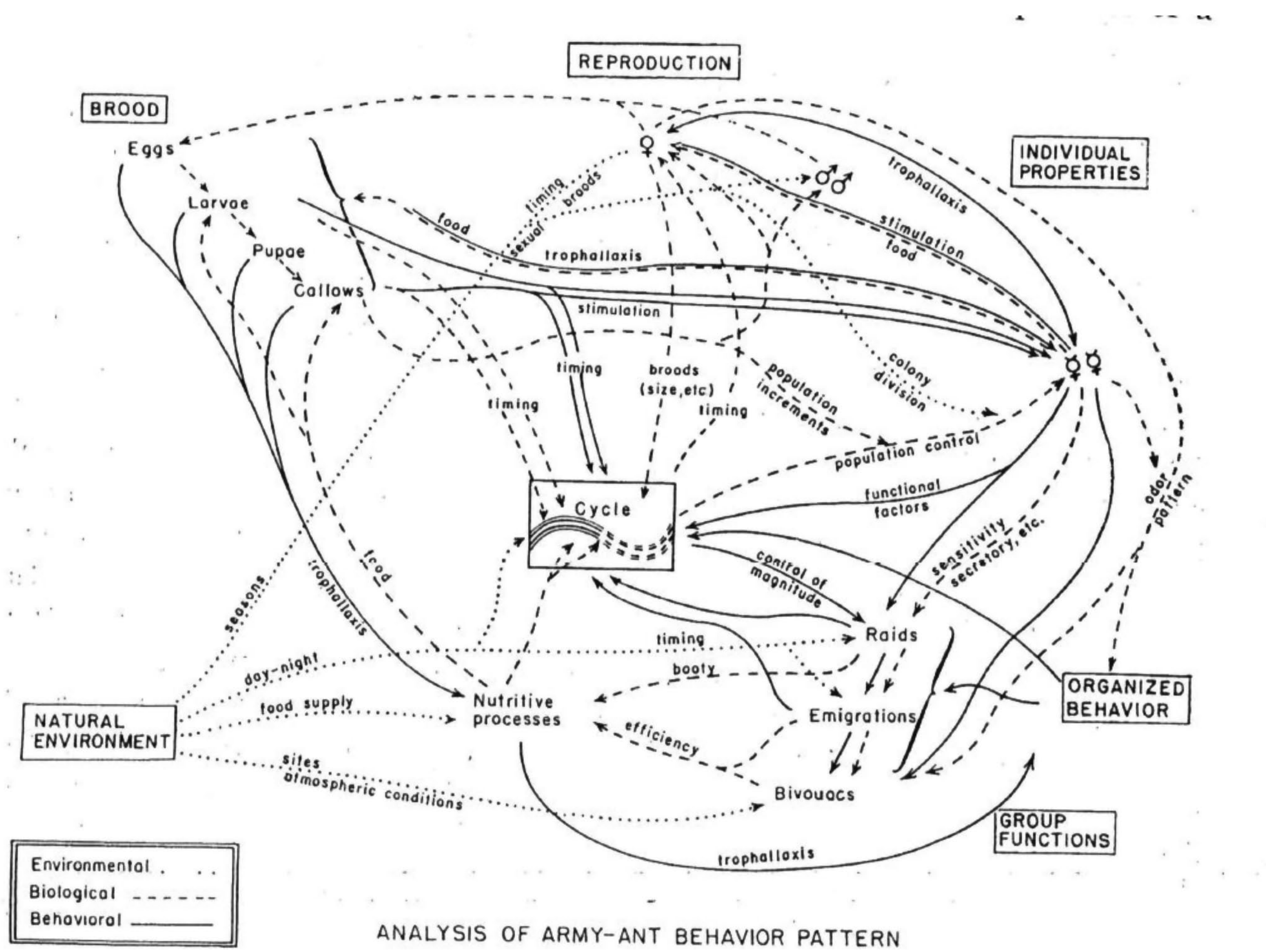

Fig. 2 A map of the "causal nexus" of factors shaping the transition from stationary to nomadism in army ants. Taken from Schneirla (1956, Fig. 1)

Doryline ants exhibit a cyclical patterning of social interactions where the colony transitions from a stationary to a nomadic phase. During the stationary phase, the colony occupies a sedentary position in the forest with periodic raids in the local area for food. In the nomadic phase, the whole colony undergoes nightly emigrations to a new area. At first, it was thought that the transition to the nomadic phase was driven by an innate response to the lack of food in the environment. However, as outlined in his posthumous book *Army Ants*, Schneirla showed that when viewed prospectively, a much richer picture of these transitions emerges (Schneirla 1971).

By describing the relationships that occur in the colony before the nomadic–stationary transitions, and documenting which relationships cause the transition to occur, Schneirla was able to map which factors played necessary roles in the stationary–nomadic transitions. During his field studies, he saw that patterns of larval development in the colony predictably preceded transitions between nomadic–stationary phases across a range of different species. From here he hypothesized that stimulation from the developing broods provided one impetus for transitions. In particular, as pupae develop they stimulate activity among workers leading to more frequent and vigorous food raids until these raids reach a threshold and the whole colony transitions to a new area beginning a new nomadic phase.

Schneirla's research on ant colonies eventually showed how a multitude of factors within and outside each individual's chitinous exoskeleton shapes colony behavior. While reciprocal interactions between the queen, new broods, and worker ontogeny were particularly important, they were embedded in larger environmental contexts. Figure 2 here, from Schneirla's (1956) paper, maps the extent of these interactions. As evident from this schematic, Schneirla did not privilege any one factor in the system: there was no controlling center or program that prefigured this transition, it rather emerged based on a historical sequence of interactions necessary to it. As he wrote, the

> cyclic pattern, therefore, arises through the diverse interrelationships of its component processes,—the morphological, physiological, behavioral and environmental factors which interact under given conditions. The organization does not pre-exist in the heredity of any one type of individual,—workers, brood or queen—, nor is it additive from these alone (Schneirla 1956, p. 401).

This example highlights the advantages of the prospective developmental approach. Without this approach, the behavior of the colony would have been relegated to innate responses to food deprivation. However, by describing the system step-by-step as it unfolds, and using targeted experiments to uncover the causal structure underlying these steps, a richer picture of development blossomed. And herein lies one of Schneirla's main points, that the innate–acquired dichotomy creates barriers rather than windows into our understanding of development. By moving beyond this dichotomy, we can open new empirical approaches to understanding both development and—as I will discuss next—evolution of behavior.

Constructive Experiences and Evolution

Behavior doesn't fossilize, and thus the ability to compare behavioral similarities and differences across living species is critical to understanding behavioral evolution. Despite this, *how* to judge behavioral similarities and differences across species and taxa has been contested. For ethologists such as Heinroth and Lorenz evolutionary relationships were inferred based on similarities in the structure of behaviors. Within neuroscience, evolutionary relationships are assumed to reflect similarities in neural circuitry, and evolutionary biology and behavioral ecology patterns of genomic divergence are linked to behavioral differences. A common thread across all these approaches is that they treat aspects of the organism—be it behavior, the nervous system, or the genome—as an innate trait, and it was this innateness that provided the stable foundation wherein comparisons between species could lead to evolutionary insights.

Nevertheless, the tenuous ontological position of innateness is an inadequate basis for comparison. Through his rejection of the innate–acquired dichotomy, Schneirla also introduced a new perspective on behavioral evolution. He claimed that comparisons made solely on the structure of behavior or its genetic underpinnings ignored the developmental processes leading to that behavior. In many cases, behaviors shared across closely related species are constructed via distinct ontogenetic processes, while in other cases very similar experiences result in divergent behavioral outcomes. Recent studies have even shown that large shifts in a population's genetic constitution can occur with no observable changes in behavior. As such, when looking at behavioral evolution one is left with one shared factor that unites all behavior: that *all behavior develops*.

But how can we compare behavioral development across species? In the featured paper Schneirla highlights how species differ in the extent to which experiences shape behavior. When discussing differences between a hydra and a cat, he notes that the range of behavioral states that can potentially develop is very narrow for the hydra but quite diverse for the cat.

> The developmental system of the mammal therefore may be termed plastic in the sense that under appropriate conditions one or more patterns differing from the species norm may be produced and retained. But in the coelenterate pattern, variability occurs about a fixed axis, at it were, and is not to be confused with plasticity. (Schneirla 1956, p. 395)

Cats, therefore, show a greater degree of behavioral plasticity than coelenterates, as when one is placed in a novel context it can create novel behaviors. Behavioral plasticity captures the range of novel behavioral states that could develop, and differences in behavioral plasticity occupy a central role in Schneirla's discussions of evolution, as they provide a means to compare development across species without the need for innate structures. He states:

> In both organisms, intraorganic relationships introduced through growth influence further stages and the outcome. But in the coelenterate these are held within narrow limits, whereas in the mammal, through wider and more complex intrinsic and extrinsic interrelationships, they become major factors in behavioral development. (Schneirla 1956, p. 394)

Today, research linking behavioral plasticity to behavioral evolution is thriving. The ability of organisms to make developmental accommodations to real-time challenges is seen as an important factor in determining their evolutionary potential. Methods such as reaction norms are commonly used to assess differences in behavioral plasticity, and studies in the field investigate how differences in plasticity across individuals, populations, and even species contribute to their ability to adapt to novel environments and thrive. Studies of animal innovation and behavioral neophenotypes have shown that animals can respond to novel environmental challenges through the production of immediately adaptive novel behaviors (Johnston and Gottlieb 1990; West et al. 1994). Studies have shown that behavioral novelty shapes success in urban environments and can be transmitted across individuals to become characteristic traits of the group or population.

Highlighting the evolutionary potential of plasticity did not originate with Schneirla. C. Lloyd Morgan, J. M. Baldwin, C. M. Waddington, and even D. Spalding (see also M. J. West-Eberhard) suggested that plastic responses to the environment can become more and more canalized via selection until they become a species-typical characteristic (Baldwin 1896; Spalding 1875; Morgan 1896; Waddington 1975; West-Eberhard 2003). What Schneirla proposed is that developmental plasticity is not uniform but shows characteristic discontinuities across species. He emphasized that constraints that once limited plasticity can be transcended and allow for new kinds of behavioral organization to emerge.

If one were to trace a line from the earliest organisms to vertebrates one could observe transitions to new types of behavioral plasticity that built upon the previous foundations, with an increase in the complexity and plasticity of behavior. Within the featured paper we find many references to these differences in "phyletic levels" which eventually become incorporated into his theory of behavioral levels. Years after the target article was published, Tobach and Schneirla (1968) proposed a classification of broad patterns of behavioral plasticity under a hierarchy that moved from taxis, biotaxis, biosocial, psychotaxis, and psychosocial levels. While Schneirla's specific taxonomy of behavioral levels was ahead of its time, it mirrored many of the advances in comparative animal cognition and highlighted that theories of behavioral evolution did not require innateness as a starting point.

Conclusion

Today, theories of innateness are undergoing a renaissance. Popular books defend the idea that animals—including humans—come into the world with an innate behavioral toolkit that prepares them for an environment they have yet to experience. Papers in psychology, biology, cognitive science, and artificial intelligence still casually assume a hard line between the innate and the acquired defines some, or even most, of our behavior. While critiques of these concepts exist, they have fallen from the front of our view. Schneirla's paper provides a glimpse at how we can move beyond the strong innate–acquired line, not just for the sake of its empirical weakness, but because doing so benefits our understanding of the development and evolution of behavior.

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