

## HOW WILL BEHAVIORAL HOMOLOGY SURVIVE IN AN AGE OF DEVELOPMENTAL PLASTICITY?

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Attempts to incorporate evolutionary thinking into modern psychology (in the form of evolutionary psychology) and developmental psychology (in the form of nativism) have been shaped by the concept of instinct as formulated by Lorenz and his followers. This ethological concept of instinct, as classically defined, has proven inadequate to the task of explaining complex behaviors (Blumberg, 2005). Moreover, although the study of well-formed animals has long represented the dominant approach to understanding the development and evolution of behavior, an exclusive focus on them can engender the illusion that behavioral development is a highly constrained and endogenously determined process. In contrast, anomalous creatures—whether induced through physical or genetic manipulation or alteration of the developmental environment—represent alternative subjects for understanding basic processes of behavioral development (Blumberg, 2009). Critically, anomalous creatures also help us to better appreciate developmental plasticity and phenotypic accommodation. But given the extraordinary behavioral plasticity inherent in the developing animal, the question then arises: Can behavior truly provide, as Lorenz believed, a firm foundation for a science of behavioral homology?

Consider how Lorenz (1958) began his *Scientific American* article entitled “The evolution of behavior.” He begins with a conventional introduction to homology using the canonical example of forelimb bones:

A whale’s flipper, a bat’s wing and a man’s arm are as different from one another in outward appearance as they are in the functions they serve. But the bones of these structures reveal an essential similarity of design. The zoologist concludes that whale, bat and man evolved from a common

ancestor. Even if there were no other evidence, the comparison of the skeletons of these creatures would suffice to establish that conclusion.

Lorenz then makes his critical transition from bones to behavior:

Following the example of zoologists..., students of animal behavior have now begun to ask a penetrating question. We all know how greatly the behavior of animals can vary, especially under the influence of the learning process. Psychologists have mostly observed and experimented with the behavior of individual animals; few have considered the behavior of species. But is it not possible that beneath all the variations of individual behavior there lies an inner structure of inherited behavior which characterizes all the members of a given species, genus or larger taxonomic group—just as the skeleton of a primordial ancestor characterizes the form and structure of all mammals today?

Lorenz's first example of such an inherited behavior—with accompanying illustration of a dog and bullfinch—concerns head scratching produced by crossing a hindlimb over a forelimb. This behavior, he writes, is exhibited by “most birds (as well as virtually all mammals and reptiles), all of whom use “precisely the same motion!” He continues:

I do not see how to explain this clumsy action unless we admit that it is inborn. Before the bird can scratch, it must reconstruct the old spatial relationship of the limbs of the four-legged common ancestor which it shares with mammals.

In short, overwing head scratching, which is “part of their genetic heritage and is not changed by training,” is an instinct: ancient, unlearned, and hardwired.

As with so many claims about complex, and so-called instinctive behaviors (perhaps my favorite being Ernst Mayr's misguided assertion that the capacity for species recognition in cowbirds, a brood parasite, is “contained completely in the original fertilized zygote”), the reality is both more complicated and more interesting. With respect to head-scratching, Burt and Hailman (1978) observed that head-scratching in birds does not necessarily

adopt the overwing configuration. Specifically, they found that young birds typically scratch by moving a leg under a wing. In addition, even adults that use the overwing method while perching switch to the underwing method while in flight. Accordingly, Burt and Hailman suggested that a bird's preferred method depends moment-by-moment on posture, balance, and center of gravity.

Consistent with his distinct approach to classifying behavior, Hailman (1969) began his own *Scientific American* article in a way that could not be more different than Lorenz's:

The term "instinct," as it is often applied to animal and human behavior, refers to a fairly complex, stereotyped pattern of activity that is common to the species and is inherited and unlearned. Yet, braking an automobile and swinging a baseball bat are complex, stereotyped behavioral patterns that can be observed in many members of the human species, and these patterns certainly cannot be acquired without experience. Perhaps stereotyped behavior patterns of animals also require subtle forms of experience for development. In other words, perhaps instincts are at least partly learned.

Instincts were Lorenz's foundation of a science of behavioral homology, so if his concept of instinct is flawed, then a science of behavioral homology is also in trouble. Hailman—as the quotation above indicates—and many others have long believed that Lorenz's instinct concept is flawed because it does not consider the roles that development and experience play in the emergence of species-typical behaviors and in the transmission of behavior across generations. This *epigenetic* or *developmental systems* perspective has only garnered more support over subsequent decades, and it presents a stark challenge to Lorenz's notion that behaviors and skeletons provide equal insight into homology and common descent.

In my view, the ethological perspective engenders a false belief in the predetermination of complex behaviors because it focuses exclusively on species-typical behaviors in typically formed adult animals. As a consequence, developmental plasticity and phenotypic accommodation are too-often overlooked.

Consider the diverse patterns of locomotion in mammals, from quadrupedal walking, bounding, trotting, and galloping, to bipedal walking and hopping. In rodents, all of these patterns are produced and there is a clear relationship between body morphology and dominant locomotor pattern. For example, jerboas are desert rodents with very long hind legs and bipedal walking and hopping gaits (Eilam & Shefer, 1997). When considered as adults, one might think that jerboas instinctively exhibit these bipedal gaits, but studies of the development of locomotion in this species tell a different story: as newborns, jerboas have similarly proportioned limbs and they exhibit locomotor patterns that are identical to other newborn rodents; as they grow and their hindlegs grow disproportionately, their locomotor patterns change accordingly. Therefore, as Hailman might have expressed it, the bipedal instinct of jerboas is learned.

In fact, the development of locomotion in other rodents informs us about the critical link that exists between the shape, size, and proportions of our bodies and the locomotor patterns that emerge (Eilam, 1997). In the several rodent species examined thus far, all pass through a similar series of locomotor stages that reflect similar morphologies at those ages. Then, as species-typical morphologies emerge, locomotor patterns diverge. As with head scratching, posture, balance, and center of gravity—all intimately linked with morphology—determine how we walk about the world.

Demonstrating similar trajectories of body morphology and behavior does not necessarily mean that behavior flows from morphology. A diehard nativist, for example, might respond by saying that evolution ensured that both were synchronized developmentally. This is where anomalous individuals—so-called “freaks” and “monsters”—can help us move beyond correlation to causation: Hand-walking in humans with malformed legs (as in a condition known as amelia) and bipedal walking in dogs and goats with malformed forelimbs demonstrate the inherent plasticity of the locomotor system and the dependence of locomotor behavior on form.

Locomotion is ancient, universal, and of critical functional importance. If anything should conform to Lorenz's concept of instinct, it is locomotion. Nonetheless, locomotion is exceedingly plastic in response to morphological change.

In light of the above comments, it seems that the notion of behavioral homology can never be more solid than the notion of anatomical homology. Accordingly, can the concept of behavioral homology survive in an age of developmental plasticity and phenotypic accommodation?

Contrary to what Lorenz hoped and believed, behaviors are not bones. In fact, based on recent developments in evolutionary developmental biology, even bones are not what they used to be. I am referring to the concept of "deep homology," which has blurred the once-clear line separating analogous from homologous structures. Shubin et al. (1997) describe deep homology in this way:

Determination of whether two structures are homologous depends on the hierarchical level at which they are compared. For example, bird wings and bat wings are *analogous as wings*, having evolved independently for flight in each lineage. However, at a deeper hierarchical level that includes all tetrapods, they are *homologous as forelimbs*, being derived from a corresponding appendage of a common ancestor.... Furthermore, we propose that the regulatory systems that pattern extant arthropod and vertebrate appendages patterned an ancestral outgrowth and that these circuits were later modified during the evolution of different types of animal appendages. Animal limbs would be, in a sense, developmental 'paralogues' of one another; modification and redeployment of this ancient genetic system in different contexts produced the variety of appendages seen in Recent and fossil animals.

Shubin and colleagues are expressing the conventional Evo-Devo perspective that places preeminent control with genes or "genetic systems." In contrast, Newman and Muller

(2000) also promote an evolutionary developmental perspective within the context of epigenetic processes:

We propose that a synthetic, causal understanding of both development and evolution of morphology can be achieved by relinquishing a gene-centered view of these processes. This is not to say that programmed gene expression plays an unimportant role during embryogenesis, or that random genetic change is not a major factor of evolution. But we argue, in agreement with some earlier writers..., that these factors are not explanatory of morphology in either of these settings. What replaces gene sequence variation and gene expression as morphological determinants in our framework are epigenetic processes: initially the physics of condensed, excitable media represented by primitive cell aggregates, and later conditional responses of tissues to each other, as well as to external forces. These determinants are considered to have set out the original morphological templates during the evolution of bodies and organs, and to have remained, to varying extents, effective causal factors in all modern multicellular organisms.

What we see today, then, are multiple currents of thought shifting and upending long-held perspectives. We are in the midst of a period of reintroduction of development into evolutionary thinking and a growing belief that systems—not just genes—are the target of selection. As a consequence, we are still learning about the development and evolution of basic morphological characters. And to the extent that morphology is a key foundation for behavior, the once seemingly rock-solid foundation for behavioral homology that Lorenz provided seems now a little shaky.

It seems that a successful science of behavioral homology will depend on the identification of appropriate behaviors as candidates for evolutionary study. To that end, we should be careful and explicit when using the term ‘instinct’ (indeed, to what extent does a sound science of behavioral homology depend on the concept of ‘instinct?’). And we will also need to be very clear about what it is about a behavior that we are trying to identify as homologous. After all, behaviors can be analyzed as *motor patterns*, as actions with

*functional outcomes*, and for the *motivations* that are presumed to fuel them. In that regard, consider that an animal without limbs will devise novel ways to scratch an itch, just as it will devise novel ways to move about the world.

If species-typical behaviors develop under the guidance of species-typical and individual experiences, then our goals should include a better understanding of the biases and constraints that guide the development of those behaviors. Specifically, I believe that we should be seeking insight into the epigenetic *processes* that shape bodies and brains and, ultimately, the development of complex behaviors. It may be in those processes—certainly not in a static chunk of DNA—that a science of behavioral homology can be found. Once armed with these insights, we should be better positioned to make claims about the developmental and evolutionary causes of behavioral similarities and dissimilarities across species.

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