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How We Develop

Developmental Systems and the Emergence of Complex Behaviors

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*“Research in such domains as fetal development, neuroplasticity, the functional organization of the brain, and cognition suggests that the old debates about **nature and nurture** should be thrown out in favor of something new — a unified ‘developmental systems’ perspective.”*

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Development evolving: the origins and meanings of instinct

Mark S. Blumberg^{1,2,3*}

How do migratory birds, herding dogs, and navigating sea turtles do the amazing things that they do? For hundreds of years, scientists and philosophers have struggled over possible explanations. In time, one word came to dominate the discussion: *instinct*. It became the catch-all explanation for those adaptive and complex abilities that do not obviously result from learning or experience. Today, various animals are said to possess a survival instinct, migratory instinct, herding instinct, maternal instinct, or language instinct. But a closer look reveals that these and other ‘instincts’ are not satisfactorily described as inborn, pre-programmed, hardwired, or genetically determined. Rather, research in this area teaches us that species-typical behaviors *develop*—and they do so in every individual under the guidance of species-typical experiences occurring within reliable ecological contexts. © 2016 Wiley Periodicals, Inc.

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INTRODUCTION

Every complex behavior challenges us to identify its origins. How do birds know to migrate south for the winter? How do border collies know to herd sheep? How do sea turtles find their way back home to the beach on which they hatched? As a shorthand—as an aid to communication—we might talk about a migratory instinct, a herding instinct, or a homing instinct. Such labels may seem gratifying, but it is an illusory gratification. Scratch the surface of any complex, adaptive behavior and one is confronted with a seemingly endless array of hard questions spanning evolutionary and developmental time, the intricacies of ecological and social experience, and the machinations of the nervous system with its billions of neurons. The more we dive into these

matters, the harder it is to settle on any clear notion of what an instinct actually is. As Patrick Bateson¹ has pointed out, this conceptual confusion about *instinct* is reflected in the many meanings that are routinely ascribed to it, including:

- present at birth,
- not learned,
- developed before it is used,
- unchanged once developed,
- shared by all members of a species,
- adapted during evolution,
- served by a distinct module in the brain,
- attributable to genes.

Scientists often unknowingly invoke more than one of these meanings at any given time, and may even unwittingly switch between meanings in a single article. This is not just a matter of lazy thinking. The murkiness of the term reflects actual confusion about the subject. No one doubts the existence of species-typical behaviors, and we can all agree that any science of behavior must endeavor to make sense of them. But there is an unsettling gulf between widely accepted assumptions surrounding *instinct* and the actual science available to explain it.

Additional Supporting Information may be found in the online version of this article.

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THE ETHOLOGICAL APPROACH TO INSTINCT

The modern study of instinct began in the 1930s with the emergence of ethology. Ethology is a sub-discipline of zoology devoted to understanding behavior in its natural context. One of the founders of ethology, Konrad Lorenz, popularized this new discipline for the general public with his many famous images of ‘imprinted’ ducklings walking behind the bearded Austrian as if he were their mother. In 1973, the young science of ethology received a significant vote of approval when three of its founders—Lorenz, Niko Tinbergen, and Karl von Frisch—received the Nobel Prize in Physiology or Medicine.

Lorenz aimed to do for behavior what Charles Darwin’s evolutionary insights did for bones. Writing in *Scientific American* in 1958,² Lorenz begins with a familiar discussion of the evolution of forelimbs: ‘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’ (p. 119).

Lorenz then makes his critical transition from bones to behavior: ‘[I]s 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?’ (p. 119).

As his first example, he cites head-scratching in birds, which he observes to be perfectly consistent from bird to bird: produced by crossing a hindlimb *over the wing* so as to reach the head (Figure 1). Lorenz exclaims that most birds scratch using ‘precisely the same motion!’ (p. 120). He then turns to other vertebrates, including mammals, and notes that they also scratch in the same way. For Lorenz, only one conclusion could be drawn from similar behaviors expressed by such different animals: ‘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’ (p. 120). In other words, scratching in dogs, birds, and other animals is the ultimate instinct: ancient, pre-programmed, and immutable.

THE RESPONSE TO LORENZ

Decades of subsequent research have since taught us to be skeptical of Lorenz’s broad assertions about the origins of behavior. For one thing, head-scratching turns out to be more flexibly produced than Lorenz assumed. Burt and Hailman,³ for example, reported that small, young birds typically scratch their heads by moving a leg *under* a wing. Moreover, some adults will use the overwing method when perching and will *switch* to the underwing method in flight. Based on these and other observations, they suggested that a bird’s method of scratching depends not on pre-programmed instructions but on the bird’s posture, balance, and center of gravity *at any given moment*.⁴ Terms such as *hardwired* and *innate* gloss over the fact that scratching depends on context—on multiple factors acting in real time. By changing context, we reveal how flexible a behavior can be.

Writing in *Scientific American*, in an article cunningly titled ‘How an instinct is learned,’ Hailman⁵ challenged Lorenz’s fundamental notion of instinct: ‘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’ (p. 241). Hailman meticulously demonstrated the influence of such subtle forms of experience through his investigations of pecking in newly hatched sea gulls.

Hailman’s perspective is a forerunner to today’s *developmental systems* approach to the origins of abilities, traits, and behaviors.⁶ The striking observation that guides the developmental systems approach is that *processes*—sometimes obvious, sometimes subtle—give rise to the emergent properties of each individual’s behavior. DNA plays a critical role in these processes, but does not by itself create traits. Accordingly, instincts are not preprogrammed, hardwired, or genetically determined; rather, they emerge each generation through a complex cascade of physical and biological influences.^{7–9} (This process-oriented developmental perspective is has long been referred to as *epigenesis*. This term should not be confused with *epigenetics*, which refers specifically to the study of how non-genetic factors influence gene expression. See Moore, Behavioral epigenetics, *WIREs Syst Biol Med*, also in the collection *How We Develop*.)

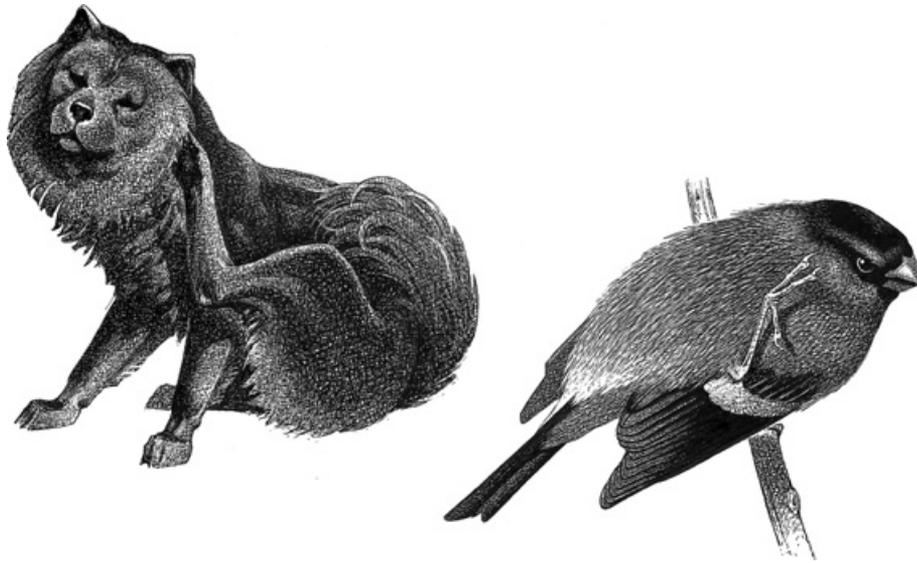


FIGURE 1 | Head-scratching in a dog and a European bullfinch. Konrad Lorenz used scratching in these two very different species to argue for the notion that behavior is shaped by evolution. With respect to head-scratching, he stated unequivocally that it ‘is part of their genetic heritage and is not shaped by training’ (p. 119). (From Ref 2. Drawings by Rudolf Freund and used with permission of Susan Freund Borden)

Lorenz’s instinct concept did not adequately consider the roles that development and experience play in the emergence of species-typical behaviors and in the transmission of behavior across generations. Even Lorenz’s explanation for the phenomenon that is most closely associated with him—visual imprinting in ducklings—has undergone significant modification over the years. Although Lorenz believed that hatchlings come into the world equipped with a single learning program that simply needs to be activated by an appropriate stimulus, subsequent research shows that imprinting comprises two independent processes.¹⁰ The first process entails a predisposition for chicks to orient toward stimuli that resemble the head and neck region of a generic mother hen; under natural conditions, this predisposition typically results in the chick orienting toward its own mother. The second process entails the acquisition of detailed information about the stimulus; again, under natural conditions, this process typically results in the chick learning about its mother. Interestingly, this two-process model has been applied to the problem of how human infants develop their ability to recognize faces (for a recent review, see Johnson et al.¹¹)

Gilbert Gottlieb spent much of his career investigating another form of imprinting—*auditory* imprinting—in which newly hatched chicks and ducklings are attracted to the mother’s call.⁸ Because the behavior of hatchlings seemed to be expressed without any obvious experience with the mother or her call, this adaptive behavior was thought to be an instinct. However, Gottlieb pursued this question in

a way that no one else before him had, by asking whether embryos obtain critical experiences *while still in the egg*. Amazingly, he found that they do: Embryos vocalize from within the egg, and these vocalizations shape the development of the auditory system in a way that is critical for their post-hatching attraction to the mother’s call. Gottlieb also found that he could make a hatchling of one species prefer the maternal call of another species by manipulating its earlier embryonic experiences. Thus, even *prenatal* experiences shape the development of species-typical behavior, often in subtle and non-obvious ways.

GRAVITY AS AN INHERITANCE

Inheritance was once strictly defined as the passing on, upon one’s death, of money, property, debts, and other earthly possessions. In contrast, within the biological sciences, inheritance has become synonymous with the transmission of DNA from one generation to the next. A developmental systems perspective, however, encourages a broader definition of inheritance to include all the biological and environmental factors that influence individual development, especially those that are reliably transmitted. By this view, DNA is certainly part of our inheritance, but so are all the species-specific cytoplasmic factors in the egg that are passed from mother to daughter. And so are the numerous environmental factors in which every biological system develops, including (but not limited to) temperature, oxygen, carbon dioxide, atmospheric pressure, and gravity.

Consider gravity, which exerts its effects everywhere and continually. It shapes and orders life on our planet: A tree's trunk is rooted in the ground and its leaves point skyward, where birds fly with their bellies directed back toward the ground. Behavioral responses to gravity are universally expressed, being found in unicellular organisms and mammals. For example, as many pet owners can attest, a cat falling upside-down will gracefully flip itself over and land on its paws. This *righting response* is made possible by the vestibular system, which includes an apparatus in our inner ear that detects changes in linear and angular acceleration. As a cat falls, the system detects the changes in acceleration and activates muscles throughout the body to flip the cat right-side up before it hits the ground.

Rat pups exhibit the righting response at birth. In a variant of the cat-falling-to-the-ground test, experimenters release a pup upside-down in a tank of warm water. The typical behavior of a pup in this water immersion test is to flip over immediately and land right-side up, a demonstration of an already-functioning vestibular system. But is this system a hardwired and ancient instinctive response to a perennially reliable feature of life on our planet? For researchers, this was a particularly difficult question to answer, as it is not possible to simply turn gravity on and off at will.

To circumvent this problem, April Ronca, Jeffrey Alberts, and their colleagues flew pregnant rats on the NASA Space Shuttle during a period of gestation when the vestibular system is developing.¹² These pregnant rats returned to Earth 2 days before delivering their offspring, which were then compared to 'ground controls' that were gestated normally on Earth. These researchers observed a variety of behavioral and neuroanatomical changes to the vestibular system resulting from gestation in microgravity. For example, although the ground-control pups exhibited normal responses in the water immersion test, the pups gestated in space often failed to even attempt to flip over, falling to the bottom of the tank on their backs (see Video 1).

Interestingly, after a week of experience in Earth's gravity the pups' righting responses were no longer impaired, which raises the question of whether isolation from Earth's gravity across the entire period of vestibular system development would lead to more lasting effects. Regardless, the lesson from this research is clear: As with Gottlieb's mallard ducklings, the presence of complex and adaptive behavior at birth tells us very little about the developmental importance of environmental factors to that behavior. Clearly, even the 'simplest' instincts develop, and

do so in response to numerous factors that we inherit from our parents, including the gravitational environment of our parents' home planet.

ANOMALOUS INDIVIDUALS AND DEVELOPMENTAL PLASTICITY

Ethology generally emphasizes species-typical behavior in natural settings. But focusing on the behavior of typically formed animals can also engender the illusion that behavioral development is a highly scripted and predetermined process. In contrast, the study of anomalous creatures—whether they arise through physical or genetic manipulation or alteration of the developmental environment—can provide key insights otherwise unavailable.¹³ Critically, anomalous creatures also help us to better understand the processes that guide typical development.

For example, Johnny Eck was a performer best known for his role in the 1932 cult classic movie, *Freaks*. Born with a condition known as *amelia*, his legs were exceedingly short and functionless. Like other individuals with this condition, Eck learned to walk using his hands. As he demonstrates repeatedly in *Freaks*, Eck's locomotion was fluid and graceful. Eck could walk down steps and climb ladders (<https://www.youtube.com/watch?v=z4aET2RG-G5Q>). He used his hands the way most humans use their feet.

Similarly, Faith is a dog that was born in Oklahoma City with short, functionless forelimbs (<https://www.youtube.com/watch?v=oSB9aBMayxU>). As has occasionally been documented in animals with this condition, Faith learned to walk upright on her hind limbs. But this is not merely a circus trick, as Faith's body grew in such a way to make upright walking possible, including a curved spine that shifted forward her center of mass. Thus, incredibly, Faith accomplished in one brief lifetime what has long been considered the crowning achievement of human evolution. Perhaps even more striking is Duncan, a dog with missing hindlimbs that walks and runs on his forelimbs (<https://www.youtube.com/watch?v=xaM-xXgl4Bs>).

Johnny Eck, Faith, and Duncan force us to reconsider our standard ideas about normal and abnormal, typical and atypical, well formed and deformed. These individuals grew into their bodies and learned to use them in highly functional ways. In fact, the *process* by which they learned to move their bodies is no different from the process by which all animals do.

To see this, let us now return to the realm of typical development and consider the diverse patterns

of locomotion in mammals: From quadrupedal walking, trotting, and galloping to bipedal walking and hopping. Across all rodent species, all these locomotor patterns are observed and there is a clear relationship between the shape of an animal's body—its *morphology*—and the pattern of locomotion that it displays. In fact, at each stage of development, as an animal's morphology changes, its locomotor pattern changes as well.

For example, jerboas are desert rodents that, as adults, have very long hind legs and exhibit bipedal walking and hopping gaits.¹⁴ One might think that jerboas instinctively exhibit these gaits, but studies of the development of locomotion in this species tell a different story: As newborns, jerboas have similarly proportioned limbs as other rodents and they exhibit locomotor patterns that are identical to other newborn rodents with similar shapes (Figure 2). But as jerboas grow and their hind legs lengthen disproportionately,

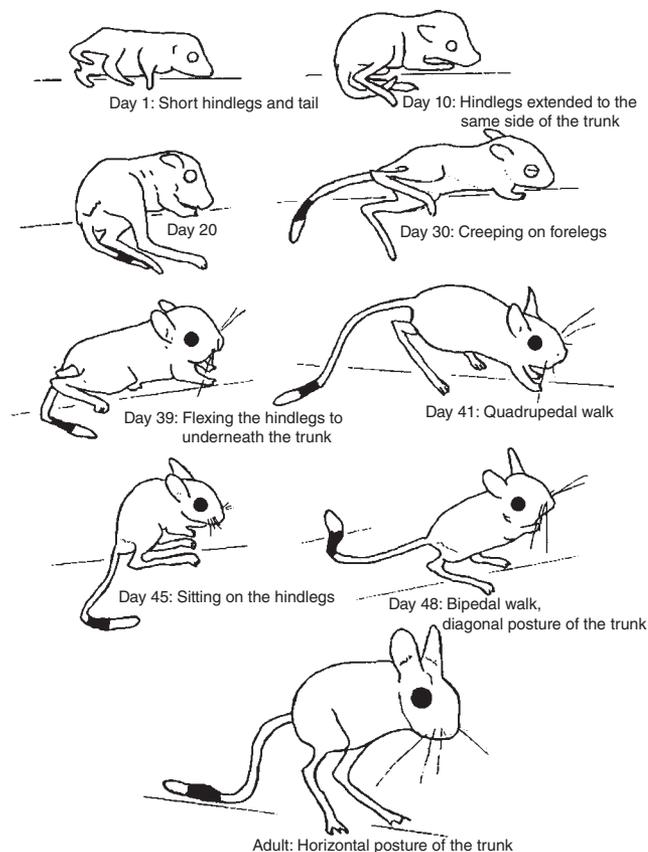


FIGURE 2 | The limbs of jerboas change dramatically across early development and their locomotor patterns change in lock-step. As newborns, these desert rodents look much like other rodents and they move around similarly as well. As their hind legs elongate, they crawl around very awkwardly. Finally, with gaining strength, they can walk and hop upright. (Reprinted with permission from Ref 14. Copyright 1997 John Wiley & Sons)

their locomotor patterns change accordingly. Specifically, as the hind legs grow longer than the fore legs, jerboas pass through an awkward stage where they struggle to accommodate their overly long legs. Later in development as their hind legs gain strength, they are able to lift themselves up and walk and hop about.

In other rodent species, such as rats and gerbils, we see similar patterns relating the shape and size of a body to the locomotor patterns expressed.¹⁵ All rodent species examined thus far pass through a series of locomotor patterns that reflect their specific morphologies at each age. As bodies change and species-typical morphologies emerge, locomotor patterns diverge. As with head-scratching in birds, posture, balance, and center of mass—all intimately linked with morphology—determine how we move.

Demonstrating close correspondences between body morphology and behavior does not necessarily mean that behavior flows from morphology. A skeptic might respond by saying that evolution ensured that behavior and morphology develop in a synchronous way without actually influencing one another. But let us not forget Johnny Eck, Faith, and Duncan: the locomotor patterns in these individuals cannot be due to any pre-programming of behavior because their behavior reflects unique solutions to unique, species-atypical bodies. In other words, individual behaviors emerge from individual development. Whether typically or atypically formed, we all must learn through individual experience to use the bodies that we have—not the bodies that we were ‘supposed’ to have.

CONCLUSIONS

History teaches us that we always learn important, critical details about a behavior by asking about its development. When Gottlieb saw that hatchlings are attracted to the maternal call, he could have stopped his investigation there and simply labeled the behavior an instinct. Instead, he asked the next question, revealed the developmental process that gives rise to the behavior, and ultimately taught us something general and profound about the nature of development and its often nonobvious causes.

Species-typical behaviors can begin as subtle predispositions in cognitive processing or behavior. They also develop under the guidance of species-typical experiences occurring within reliable ecological contexts. Those experiences and ecological contexts, together comprising what has been called an *ontogenetic niche*, are inherited along with parental genes.¹⁶ Stated more succinctly, environments are inherited—a notion that shakes the nature–nurture

dichotomy to its core. That core is shaken still further by studies demonstrating how even our most ancient and basic appetites, such as that for water, are learned.¹⁷ Our natures are acquired.

None of this should be taken to mean that all behaviors are equally malleable. On the contrary, behaviors lie along a continuum from highly malleable or plastic to highly rigid or robust¹⁸ (see Bateson, Robustness and plasticity in development, *WIREs Cogn Sci*, also in the collection *How We Develop*). Our challenge, then, is to move beyond the age-old practice of applying dichotomous labels to

behaviors.¹⁹ Instead, we should seek to understand the developmental contexts and conditions that make a behavior more or less malleable.

So the next time you see a marvelous and complex behavior—such as a border collie herding sheep or birds flying south for the winter—try to resist the temptation to label it as *instinctive*, *hardwired*, *genetic*, or *innate*. By foregoing a label and digging deeper, you will open yourself to consideration of the myriad of factors that shape who we are and why we behave the way we do.

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