Behavior

Citation: Lahti, D. C. 2018. Behavior. *Inference: International Review of Science* **3** (4).

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Behaving: What's Genetic, What's Not, and Why Should We Care?
by Kenneth Schaffner
Oxford University Press, 304 pp., USD$74.00.

Biology / *Book Review*

Questions about the causes of behavior raise longstanding concerns in biology. What is genetic and what is environmental? In *Behaving*, Kenneth Schaffner addresses this question, drawing on insights from psychiatry, behavioral genetics, and the philosophy of science.

At its best, *Behaving* is a survey of current behavioral genetics applied to *Homo sapiens* and the nematode *Caenorhabditis elegans*. The first third of *Behaving* discusses the two methods currently used to understand genetic action. Quantitative genetics looks to the overall similarities in twins and families to provide indirect evidence for links between genetic variation and behavior. Molecular genetics analyzes the genome for more direct evidence.

The middle section of Schaffner's book introduces *C. elegans* through a selection of studies responding to historical concerns about behavioral genetics. Some question the utility of reductionism, the attempt to understand behavior in terms of its components. Others propose that genes are one among a string of causes, and do not enjoy a privileged place in the overall system that produces behavior.

In the final section of *Behaving*, Schaffner examines genetic research on psychological conditions. Although disappointed by progress in this field as a whole, he is more optimistic about schizophrenia research, going so far as to delay the publication of his book to incorporate the latest genome-wide association studies (GWAS). Such studies represent a clear departure from narrowly focused research on specific but influential genes, in favor of a broad scan of the genome in the hope of discovering correlations with psychiatric diagnoses. In the case of schizophrenia, GWAS have been unusually clear and forthcoming. Yet we still do not have have anything close to a causal narrative connecting genes to behavior.

Why should we care about the role of genes in behavior? This is, after all, the subtitle of Schaffner's book. That we care about free will is one answer. Schaffner tentatively endorses a compatibilist view: despite genetic influence, our agency is real and it is one of the causes of behavior. Schaffner offers four reasons for his conclusion: most of our behavior appears to be influenced by thousands of genes of very small effect; their action is conditioned by the environment; genes work through "partially probabilistic neural networks";[1] and free will accords with our individual experience.

A healthy level of skepticism prevails throughout *Behaving*. Candidate genes have made modest inroads, but nothing that justifies labels such as the warrior gene or the gay gene. Most behavioral traits will likely be traced to hundreds, or even thousands, of genes. Schaffner believes that even recent GWAS fails to explain the fact that the accumulated effect of known genetic variants still falls short of what we expect based on estimates of heritability. Schaffner suggests that we focus on higher level, cross-pathway interaction effects, somewhat like the way we explain gases by assessing the effects of temperature and pressure on volume, as in the perfect gas laws.

What *Behaving* does not offer is a sense of the bigger picture. In the overall science of behavior, behavioral genetics is a rather technical subfield. Any talk of genes and environment only makes sense in the broader context provided by development and evolution. Development is the story of an individual living thing. Genes and the environment are two different sources of information, but they do nothing by themselves. Development is the process by which they become integrated into a growing organism. Development reminds us that genes and the environment are close collaborators rather than opposing powers.

When an animal, such as *C. elegans*, is initially developing, the spatial position of a cell in an embryo determines which part of the body it will ultimately become. Each cell has the same complement of genes. Most will be expressed in all cells, but differently in different places. Despite identical genes, environmental cues lead to radically different cellular fates. Yet the genes still control development. Most of the same genes expressed initially are also expressed in the sexually mature adult, although quite differently at each stage. Even the behavioral plasticity of *C. elegans* is modulated by specific genes, which connect the animal's perception of its environment to its behavior.[2] The questions posed in the subtitle of Schaffner's book are misleading. Everything is genetic and nothing is not. Genes and the environment are not opposing or alternative explanations for behavior. Development is the manifestation of an interactive relationship between genes and the environment.

Behavior, in comparison with traits such as eye color, height, or bone density, is unusually plastic. The more plastic a trait, the more complex the interaction between genes and the environment in its development, and the greater the challenge faced by geneticists. "Heredity is particulate," Theodosius Dobzhansky remarked, "but development is unitary."[3] A diverse array of information or influences, not only from genes but also the environment, must filter, mutually combine, and funnel into a unified process, a singular organismal lifetime. Development is the story of this integrative shaping.

By neglecting development, biologists once marginalized or ignored important genetic phenomena such as polygenic inheritance, where many genes operate on a single trait, pleiotropy, where one gene does many things, and epistasis, where genes affect each other. These features are ubiquitous. They are the rule rather than the exception.

In *Behaving*, Schaffner laments the absence from biology of predictive explanatory theories like those that can be found in physics. On the contrary, we do have a theoretical framework that makes sense of behavior and explains why organisms do one thing rather than another. This framework is the theory of evolution. Descent with modification and natural selection produce general predictions that, when applied to particular organisms and traits, can become remarkably specific. Behavioral predictions follow from our understanding of evolution, completely apart from the particulars of the interaction of genes and environment in development. Only by applying evolution to the study of behavior can we progress beyond an open exploration of model systems.

If the environment remains constant across several generations, and a particular behavioral strategy is optimal, evolutionary theory predicts that this strategy is apt to be inherited, not learned. In a population of individuals competing for limited resources, inheritance wins by natural selection because it is more reliable and less costly than learning. If the environment is variable, organisms are expected to evolve a particular inherited relationship between an environmental feature and behavioral development. If environmental change is slow in relation to an organism's lifetime, behavioral calibration is expected to be performed only once and irreversibly, usually at the beginning of life. In the presence of predators, for example, tadpoles develop tails helpful for high-speed escapes. If the environment is safer, they develop more agile tails that make them better competitors for food. If, on the other hand, the environmental conditions vary predictably over the course of a lifetime, an organism should evolve back-and-forth behaviors, as when animals aestivate when it is hot and hibernate when it is cold.

Adaptive plasticity can develop in a variety of ways. Zooplankton make a daily vertical journey through the water column, thereby optimizing factors such as metabolic efficiency, their exposure to UV light, and their ability to avoid predators. Not much cognition is required. The inherited genes of zooplankton guide the development of a nervous system that operates almost as if it were coded with *if-then* and *for-next* loops.

Significant changes in the environment are sometimes too numerous, rare, or novel for any simple form of neural programming. In such environments, organisms have evolved the cognitive capacity to construct associations in real-time between environmental features and outcomes. Learning is the most fascinating form of plasticity. Guided by older predispositions, learning evolves against an inherited backdrop of automatic responses or simple heuristics. This is true even of advanced forms of learning. Psychological biases have evolved to shape learning programs for particular behavioral ends.

For the last four decades, evolutionary biologists have been working to explain social learning. Bird song is the best-studied learned behavior in nature. Although the development of bird song is also guided by inherited factors, songbirds learn to sing from one another; their singing functions in mate choice and competition. Changes can accumulate in the social transmission of behavior, either through mistakes in copying, or by individual innovation. Human language and bird song change subtly over generations, resulting eventually in great diversity. Current research seeks to determine whether such cultural evolution operates by reliable rules, and whether they are similar to the rules governing genetic evolution. Cultural evolutionists differ on the extent to which natural selection has shaped patterns of social transmission.

Some psychologists have expressed concern that an evolutionary perspective might minimize the role of the environment. Evolution, on the contrary, allows us to understand the roles of the environment and learning, and relate them to the other components in the development and production of behavior, including the genes. The environment shapes behavior within a lifetime through evolved plasticity, including complex learning. Across lifetimes, the longest-running environmental influence of all is natural selection. Concerns about genetic determinism are outdated and based on a non-developmental, pre-evolutionary understanding of behavior. Genes are one component of an integrated system. We should be no more concerned about genetic determinism than we should about evolutionary, developmental, or environmental determinism.

The more mysterious and often troubling matter of free will remains. No will remains unaffected by external influences. We are misguided if we expect immunity from our evolutionary heritage. Both genes and the environment affect our personality, morality, and sexuality. Since we evolved from organisms with less plasticity than ourselves, the older our features, the less our control over them. Cultural mores may be adopted or discarded, but deeper social features can be modified only with tremendous effort or in the context of a highly unusual environment. Hormonal levels and neuronal connectivity are even more resistant to wilful manipulation. The deepest mammalian or vertebrate features are here to stay.

Whatever the *will* is, it is hardly free.

Nevertheless, our agency at its root is not undermined by behavioral genetics, nor by evolutionary biology, nor by any other science. In *The Selfish Gene*, Richard Dawkins asserted that we are “robot vehicles blindly programmed to preserve the selfish molecules known as genes.”[4] This statement served to explain natural selection. Dawkins intended his remark to be taken with a grain of salt. In the last chapter of *The Selfish Gene*, Dawkins encouraged rebellion against that blind program.

If our genes blindly dictated particular behaviors, we would be highly maladaptive in our complex and competitive world. Our brains have evolved an ever-increasing plasticity, a broadening of the scope of influential inputs and behavioral outputs. On a daily basis we look far further into the future, far more deeply into the past, and far more closely into the minds of other people than any other species living or dead. This is not by coincidence. Such intelligent diversification of our portfolio of behavioral influences has been adaptive in our competitive ultrasocial milieu, and has contributed to our mastery of the planet.

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1. Kenneth Schaffner, *Behaving: What’s Genetic, What’s Not, and Why Should We Care?* (New York: Oxford University Press, 2016), 244.
2. For relevant summaries, see Bruce Alberts et al., “*Caenorhabditis Elegans*: Development from the Perspective of the Individual Cell,” in *Molecular Biology of the Cell*, 4th ed. (New York: Garland Science, 2002); and Oliver Hobert, “Behavioral plasticity in *C. Elegans*: Paradigms, Circuits, Genes,” *Journal of Neurobiology* 54 (2003): 203–23.
3. Theodosius Dobzhansky, in *Insect Polymorphism*, ed. J. S. Kennedy (London: Royal Entomological Society, 1961), 111. Richard Alexander often remarked that this is one of those simple statements that one could digest for hours in order to more fully understand its importance, e.g. Richard Alexander, “Darwin’s Challenges and the Future of Human Society,” in *Predicting the Future in Science, Economics, and Politics*, eds. Frank Wayman et al. (Northampton, MA: Edward Elgar, 2014), 78.
4. Richard Dawkins, *The Selfish Gene*, 30th anniversary ed. (Oxford: Oxford University Press, 2006), xxi.