



Editorial: The Many Faces of Behavioral Evolution



Behavioral evolution results from three general processes across three different timescales: genetic evolution across generations, individual learning and development within generations, and cultural evolution within and across generations. We usually think of individual learning and development and cultural evolution as nested within genetic evolution. However, these evolutionary processes interact. Through gene-culture co-evolution, cultural processes can drive genetic evolution. Through genetic assimilation, individual learning repeated across many generations can result in genetic change.

Although many disciplines study behavioral evolution, including behavior analysis, evolutionary anthropology, and evolutionary biology, for the most part each discipline focuses on just one process and timescale of behavioral evolution. The typical behavioral analyst studies how the environment shapes the behavior of individual organisms. The typical anthropologist studies how environment shapes the cultures of groups of people. And the typical evolutionary biologist studies how ecology shapes genetic populations. Of course, this characterization is caricature. Countless researchers have pursued and pioneered research that studies the interaction among adaptive processes. Skinner (1981), for example, described the parallels between genetic evolution, behavioral evolution, and cultural evolution. Boyd and Richerson (1985) have explored how genetic evolution gives rise to the capacity for culture, how cultural evolution arises from individual psychology, and how cultural processes can drive genetic evolution. Building on the work of Boyd and Richerson and others, Baum (2017) described how genetic evolution, cultural evolution, and individual behavioral evolution all interact to produce human behavior.

For this special issue of *Behavioral Processes*, we brought together a diverse group of researchers from a range of disciplines, including biologists, anthropologists, and psychologists, and also economists, historians, and computer scientists. Our hope was to foster cross-disciplinary communication and even collaboration. Many of the contributions to this special issue are not the typical journal fare consisting of a narrowly-developed theoretical argument or a carefully-designed experimental or observational study. Instead, we invited authors to explore, sometimes speculatively, the connections and interactions among different evolutionary processes and timescales. We are grateful to *Behavioral Processes* for allowing us the opportunity to put together this kind of special issue. We hope that at least some of the papers will generate discussion and inspire intellectual innovation.

A psychologist, an anthropologist, and a computer scientist meet online for the first time. No, this isn't the set up to a joke. Instead, it describes the origins of one of the papers in this special issue. In "Enriching Behavioral Ecology with Reinforcement Learning Methods", Frankenhuysen and Panchanathan, who previously collaborated on building evolutionary models of development, wrote a paper with Andrew Barto, a computer scientist who pioneered research on

reinforcement learning, on the connections between theoretical research in behavioral ecology and reinforcement learning. This paper, and others in this special issue, resulted from our invitation for authors to seek out new collaborators and explore new research topics. The paper by Simon and Hessen ("Selection as a Domain-General Evolutionary Process") brought together a behavior analyst and an evolutionary biologist, who argued that selection may be seen as an extremely general mode of causality, at every scale of life. In "Pathways to Cognitive Design", Wertz and Moya, a psychologist and an anthropologist, articulate how researchers in evolutionary psychology and cultural evolution approach the study of design. And in "Zoon Politikon: The Evolutionary Origins of Human Socio-political Systems", Gintis, van Schaik, and Boehm, respectively an economist, a primatologist, and an anthropologist, explore the origins of political psychology and behavior.

Other articles in this special issue explore the connections between different levels of explanation (Tinbergen 1963). Four of the contributions examine more closely ontogenetic behavioral evolution by selection in the context of broader understanding of the interaction between phylogeny and ontogeny. These include Simon and Hessen ("Selection as a Domain-General Evolutionary Process"), Becker ("The Flight of the Locus of Selection: Some Intricate Relationships between Evolutionary Elements"), Killeen ("The Non-Darwinian Evolution of Behaviors and Behaviors"), and Rachlin ("Group Selection in Behavioral Evolution"). Smith ("The Roles of the Analogy with Natural Selection in Skinner's Philosophy"), Burgos ("Selection by Reinforcement: A Critical Reappraisal"), and Clark Barrett ("Selected emergence in the evolution of behavior and cognition") explore philosophical aspects of the interaction between natural selection and developmental processes.

The remaining five papers address novel topics in the study of cultural evolution. In "State-dependent cognition and its relevance to cultural evolution", Nettle argues that cultural evolutionary theory might benefit by borrowing from behavioral ecology and explicitly modeling variation in state among individuals. In a similar vein, Smaldino ("Social Identity and Cooperation in Cultural Evolution") argues that we need to more explicitly theorize the interaction of individual social identities and cultural evolution. Koditschek ("Evolutionary Approaches to Complex, Asymmetrically Structured Societies") argues that human societies are better understood by theoretically separating cultural evolution from social evolution. And Brendan Barrett ("Equifinality in empirical studies of cultural transmission") argues that different cultural evolutionary processes can result in the same end state ("equifinality") and discusses how to empirically study such cases. Richerson ("An integrated Bayesian theory of phenotypic flexibility") explores the possibility of characterizing, not only natural selection, but cultural selection, individual learning, epigenetic inheritance, and adaptations such as the immune system as all

depending on priors that are updated as an organism faces environmental variation on different time scales.

The last three paragraphs represent one way in which we could have categorized the contributions to this special issue. There were other possibilities. This reflects our invitation and selection process. Rather than constrain authors to explore a very specific topic, we encouraged them to broadly explore behavioral evolution, particularly with regards to the interactions between individual learning and development, cultural evolution, and genetic evolution. We invited a wide range of researchers to submit conceptually, theoretically, or methodologically innovative papers, even if speculative. Whatever your field, even if some of these 15 papers seem elementary, others will be surprising and educational, because scholars in these different areas have too long labored separately. We suggest reading particularly the papers outside your area to see what other concepts you might want to incorporate into your own thinking.

Guest Reviewers for the Special Issue on Behavioral Evolution

Annie Wertz
Matthew C. Bell
Terry Smith
Christopher Stephens
Peter J. Richerson
Louise Barrett
Andrew Sih
Peter Trimmer
Alex Kacelnik
Alasdair Houston
Philip N. Hine
W. David Stahlman
Sigrid Glenn

Brendan Barrett
Daniel Nettle
Howard Rachlin
Peter Killeen
Paul Smaldino
Anne Kandler
David Geary
André Ariew
Theodore Koditschek
Matthew Zefferman
Daniel Little
Cristina Moya
Paul Smaldino
David Elder-Vass
Willem Frankenhuis
Heidi Colleran
Daniel Hruschka
Clark Barrett
Matthew Gervais
Kevin Laland

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Karthik Panchanathan, William M. Baum