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Integrating the how and why of within-individual and among-individual variation and plasticity in behavior

Suzanne H Alonzo

Although phenotypic variation within and among individuals in the same population may represent 'noise', it can also be the adaptive plasticity that allows organisms to adjust to varying environments or the heritable variation that fuels evolutionary change. Behavioral variation arises from a complex combination of adaptive and non-adaptive individual plasticity and consistency. Differentiating these sources of behavioral variation will require an integrated combination of evolutionary and mechanistic understanding. Yet, this integration comes with a variety of challenges. Here I argue that we will need concrete *a priori* predictions to make sense of the large and complex datasets this integration will require.

Address
Department of Ecology and Evolutionary Biology, University of California Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, United States

Corresponding author: Alonzo, Suzanne H (shalonzo@ucsc.edu)

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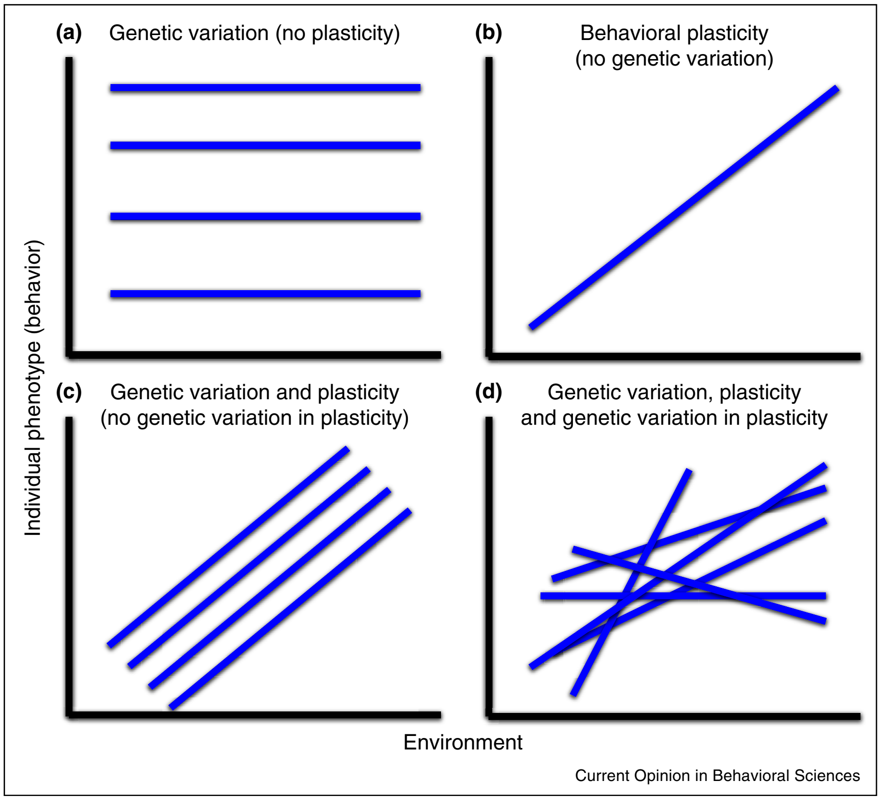
Introduction

Significant phenotypic variation exists within and among individuals in most populations, even in traits fundamentally connected to fitness such as reproduction [1–3,4•,5–8,9•,10,11]. This empirical reality has motivated extensive theory aimed at understanding the evolutionary processes that allow genetic and phenotypic variation to arise and persist [12–19,20••,21–23]. Yet our empirical understanding of behavioral plasticity (i.e. the production of different behaviors by a single genotype in response to environmental cues and conditions) remains somewhat limited by our ability to make sense of 'messy' empirical patterns [4•,9•,20••,21–23,24•,25••,26••,27,28]. How do we know if the variation we are observing is simply 'noise' (i.e. non-adaptive genetic or phenotypic variation), adaptive plasticity or heritable phenotypic variation?

At a conceptual level, the answer to this question seems simple. We need only to know whether the variation is heritable and how it affects fitness. In reality, it is much more challenging. One reason for this challenge is that real behavioral variation does not fit neatly into these simple conceptual categories (Figure 1) [6,11,18,29,30]. Instead, genetic variation for behavior and plasticity in behavior can coexist and observed patterns involve a complex mix of adaptive and non-adaptive variation [15,31]. Organisms exhibit both consistency and plasticity in behavior, and we now realize that understanding one requires explaining the presence or absence of the other [22,32]. There is also an increasing appreciation that unexplained within-individual variation (or intra-individual variability) is not just 'noise'; it can inform our understanding of selection on and the constraints underlying plasticity and consistency [20••,22,23,32–34]. Furthermore, the mechanisms underlying behavioral plasticity likely influence the fitness of plastic genotypes and an organism's ability to exhibit plasticity; these mechanisms may therefore bias, facilitate or even constrain phenotypic evolution [35,36]. Fully understanding how behavioral plasticity evolves and affects observed patterns of behavior therefore requires knowing more about the genetic and mechanistic basis of behavioral plasticity.

Here, I focus on behavioral variation and plasticity, though many of the arguments apply to other forms of phenotypic variation. I first briefly review some of the evolutionary explanations for the existence of behavioral variation and plasticity. Second, I review recent arguments for the importance of integrating evolutionary (i.e. ultimate or why explanations) and mechanistic (i.e. proximate or how explanations) perspectives in the study of behavior and suggest that concrete evolutionary theory incorporating the genetic, regulatory and neuroendocrine basis of behavioral variation is needed. Finally, I argue that if we want to truly understand the forces that shape within-individual and among-individual variation in behavior and plasticity, we need to integrate recent advances in our evolutionary understanding of behavioral plasticity and consistency with the ever-increasing knowledge of the genetic and mechanistic basis of behavioral variation and plasticity. Though challenging, the answer to the seemingly basic question of how and why individuals vary over time and from one another is fundamental to many topics in biology, including why and how the sexes differ from one another and how organisms are predicted to respond to human-induced environmental change.

Figure 1



Disentangling the basis of behavioral variation can be challenging. Each panel shows how the phenotype (such as amount of parental care provided, time spent on territory defense or courtship rate) of different genotypes (represented by blue lines) will change as a function of the environment (such as individual condition, ambient temperature or social interactions with conspecifics). **(a)** When behavioral variation is purely genetic in basis (i.e. no plasticity exists) than behavior is predicted to differ between genotypes but will not vary across environments. **(b)** When behavioral variation arises only from plasticity, then no genetic variation exists but behavior varies across environmental conditions. **(c)** Behavioral variation can arise from both plasticity and genetic variation in behavior even if variation among genotypes in plasticity does not exist. **(d)** In reality, behavioral variation likely arises from a combination of genetic variation in behavior, variation arising from plasticity and variation among genotypes in plasticity. Although panels (a) and (b) would be relatively easy to differentiate, panel (d) is most likely what actually occurs in most species. The real question is not whether variation arises from genetic variation or plasticity (i.e. a vs b), but instead how much variation in behavior is caused by genetic variation, plasticity or the interaction between the two.

The evolution of behavioral variation and plasticity

Variation among individuals in the same species can arise from a variety of sources: First, genetic variation among individuals may cause phenotype variation. This genetic variation may be neutral (e.g. arising from recent mutations or selectively neutral alleles) or adaptive (e.g. maintained by selection). Second, variation arises when identical genotypes produce different phenotypes. This phenotypic variation among individuals of the same genotype can also represent either adaptive phenotypic plasticity (e.g. phenotypic variation that increases the fitness of the genotype on average across environments) or non-adaptive 'noise' (phenotypic variation that does not increase the fitness of the genotype on average). Finally, within-individual variation in behavior can arise in response to variation in endogenous and exogenous variables over time and through development. Here, I focus on how and why adaptive variation exists within and among individuals in the same population, particularly behavioral variation arising from plasticity. It is important, however, to keep in mind that neutral genetic variation and 'noise' in the developmental or physiological systems will also produce variation within and between individuals. The challenge is to be able to tease apart how much of the behavioral variation we see represents 'noise', adaptive plasticity or heritable variation and what these patterns of variation tell us about the evolutionary basis, maintenance, and consequences of this variation.

The evolutionary maintenance of genetic variation

Selection is generally predicted to decrease genetic variation — and thus likely also phenotypic variation — because genes associated with higher fitness will increase in frequency and replace genes or genotypes associated with lower fitness [37–39]. Some genetic