The role of trade-offs and feedbacks in shaping integrated plasticity, behavioral syndromes, and behavioral correlations

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KEY WORDS

behavioral syndromes, integrated plasticity, state dependence, trade-off, feed-back

DATA AND MODEL AVAILABILITY

Model code, as well as the data associated with Figures 2 & 3, are available at github.com/DochtermannLab/FeedbacksModel. Both code and data will be made available at Dryad if accepted.

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INTRODUCTION

Despite a decade and a half of intensive research effort, we still have little understanding of why behavioral responses are frequently correlated. This gap in our understanding stems from the fact that much of the work looking into behavioral correlations has focused on among-individual correlations, i.e. "behavioral syndromes" (Figure 1A & 1B, Box 1; Sih et al. 2004a, Sih et al. 2004b, Dingemanse et al. 2010, Dingemanse et al. 2012). Unfortunately, this focus on syndromes ignores the fact that behavioral correlations are, instead, primarily due to within-individual correlations (Box 1, Figure 1C).

One contributor to within-individual correlations is "integrated plasticity" (Box 1, Table 1). Within-individual correlations include—but are not limited to—correlated plastic responses to temporary environmental variation, specifically responses to unmeasured or unmodeled environmental variation. This variation is akin to "phenotypic flexibility" (Piersma and Van Gils 2011) but integrated across multiple behaviors. Despite more

Box 1. The relationship of behavioral syndromes and integrated plasticity to behavioral correlations: the primacy of integrated plasticity

Behavioral correlations at the population and phenotypic level (r_p) emerge from the joint contributions of among-individual correlations, i.e. behavioral syndromes (r_A), and within-individual correlations (r_w, Figure 1; (Dingemanse et al. 2012)). The relative influence of each of these on observed correlations is mediated by the repeatability of the behaviors of interest (τ_1 and τ_2):

$$r_p = r_A\sqrt{\tau_1\tau_2} + r_w\sqrt{(1-\tau_1)(1-\tau_2)}$$

r_A is the statistical definition of a behavioral syndrome (Dingemanse et al. 2012) and, as repeatability decreases, the contribution of behavioral syndromes to phenotypic correlations necessarily decreases. At the extreme, if τ for either behavior is 0, then r_p is entirely determined by the r_w. Moreover, r_w contributes more strongly to r_p than does r_A when geometric mean repeatability is less than 0.5 (Dingemanse and Dochtermann 2013). Based on meta-analysis (Bell et al. 2009) we know that average τs are around 0.4 and r_w, on average, influences r_p more strongly than does r_A. Put another way, within-individual correlations have an average 1.5 times greater influence on phenotypic correlations than do behavioral syndromes.

Importantly, while r_w includes integrated plasticity, this plasticity will not necessarily be adaptive and errors both in the response to cues by organisms or in measurement also contribute to r_w (Table 1).

strongly influencing behavioral correlations than do behavioral syndromes (Box 1), within-individual correlations and integrated plasticity have received little direct theoretical or empirical attention by behavioral researchers.

Table 1. Some contributors to within-individual behavioral (co)variation and correlations. If either active or passive plasticity are elicited in response to known and measured environmental parameters, they can be explicitly modeled. Otherwise, they will contribute to within-individual variation and covariation. Similar processes contribute to the irreversible plasticity (aka developmental plasticity), which contributes to among-individual correlations (Dingemanse and Dochtermann 2014). The contribution of each component of within-individual correlations can be determined by breaking r_w down into constituent parts, similar to how a phenotypic correlation is broken down in Box 1.

	Definition	Contributes to integrated plasticity	
Active reversible plasticity	changes in an individual's behavior expressed in response to environmental cues indicative of selective pressures	**yes**	(Piersma and Drent 2003, Piersma and Van Gils 2011)
Passive reversible plasticity	changes in response to environmental conditions rather than specific cues of selective pressures; includes passive responses to abiotic conditions, such as hypoxia	**yes**	(Whitman and Agrawal 2009)
Reversible organismal error	changes to an organism's phenotype in response to an incorrectly processed cue	*no**	(Westneat et al. 2015)
Measurement error	error in quantification of behaviors; can be correlated due to bias an	*no**	(Westneat et al. 2015)

*assumes uncorrelated error. For a discussion of additional contributors to within-individual (co)variation see: (Piersma and Drent 2003, Whitman and Agrawal 2009, Piersma and Van Gils 2011, Westneat et al. 2015, Berdal and Dochtermann 2019)

One possible mechanism shaping integrated plasticity is a trade-off in investment of energy (or other resources) into behaviors. Accordingly, we would expect that as individuals positively increase investment in one behavior, they decrease investment in another (Figure 1A). Such a trade-off would generally be expected to result in negative

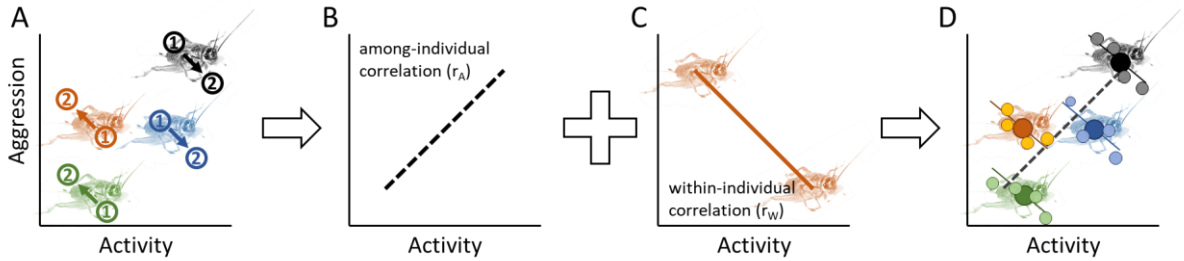

Figure 1. Example of how behavioral syndromes, i.e. among-individual correlations (r_A) and integrated plasticity, i.e. within-individual correlations (r_W), additively contribute to phenotypic correlations. A) Activity and aggressive behavior of four crickets are measured on two occasions (1 & 2). Crickets largely maintain their relative differences in each behavior (i.e. "personality") *and* their behavior changes in a correlated manner (integrated plasticity). B) The relationship among crickets is due to a positive among-individual correlation (dashed blue line, r_A). C) Behavioral plasticity is negatively correlated (within-individual correlation: solid orange line, r_W): if an *individual* increases its activity, it decreases its aggression. D) The among- and within-individual correlations additively determine average individual behaviors (dark circles) and how crickets vary from their averages (colored lines and smaller, lighter, circles). The influence of either r_A or r_W on the phenotypic correlation (solid black line in D) is determined by the repeatabilities of the behaviors. If repeatability is high (> 0.5), this phenotypic correlation is primarily determined by the behavioral syndrome, r_A (Box 1).

within-individual correlations (Figure 1C). If individuals differ in their ability to acquire resources, this results in the familiar "big house, big car" scenario from life-history theory (Van Noordwijk and de Jong 1986, Reznick et al. 2000): high variation in acquisition (relative to variation in allocation) results in a positive among-individual correlation despite underlying trade-offs. If trade-offs underpin behavioral correlations we would therefore expect among-individual and within-individual correlations between behaviors to be of opposite signs (Figure 1D; Downs and Dochtermann 2014).

Meta-analyses have examined behavioral correlations at the genetic, among-individual, and within-individual levels (Dochtermann 2011, Brommer and Class 2017). These analyses have concluded that correlations across levels are generally concordant as to their signs and magnitudes (Figure 2). This concordance of signs suggests a *potential* lack of trade-offs in the expression of behaviors or that variation in acquisition is low

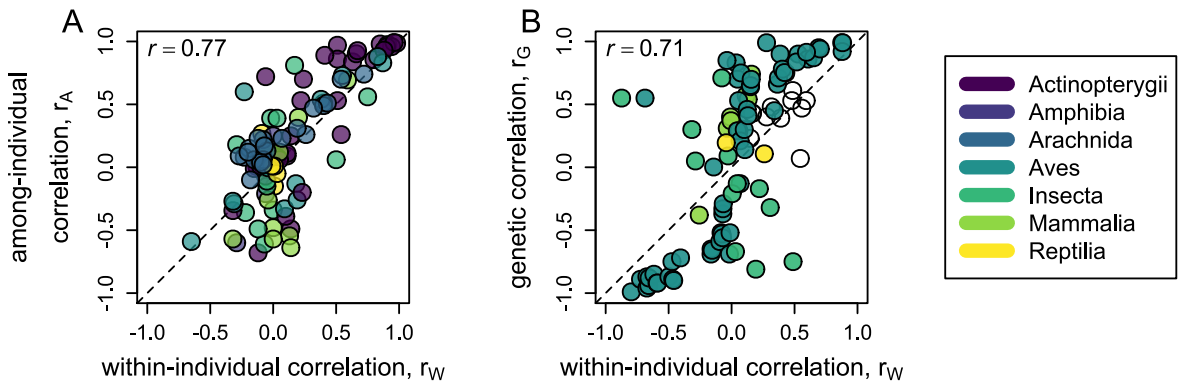

Figure 2. Relationship of within-individual behavioral correlations (r_W) with (A) among-individual correlations (r_A) and (B) genetic correlations (r_G). The sign and magnitude of r_A and r_G are highly concordant with r_W across behaviors and taxa. Dashed lines indicate a 1:1 relationships. Data in A are from Brommer and Class (2017). Data in B are from Dochtermann (2011).

relative to variation in allocation. As an important caveat, it is also possible that many of the analyzed behaviors should not be expected to trade-off due to naming fallacies obscuring that the same behavior is actually being measured in different ways (Carter et al. 2013) or because limiting resources differ between behaviors. Opposing signs may also not be predicted when considering only a few traits within a higher-dimensional phenotype (Blows and Hoffmann 2005, Blows 2007). Nonetheless, the results in Figure 2 suggest that trade-offs alone are insufficient to explain patterns of among- and within-individual correlations.

An alternative mechanism for understanding behavioral correlations builds on a simple model of trade-offs by adding in feedbacks between underlying state and behaviors. Sih et al. (2015) proposed that among-individual differences in behavior—i.e. "personality"—can be generated by feedbacks between behavior and underlying state. This was supported by a model where the intensity of initial behavioral expression resulted in a feedback shaping an individual's future behavioral expression.

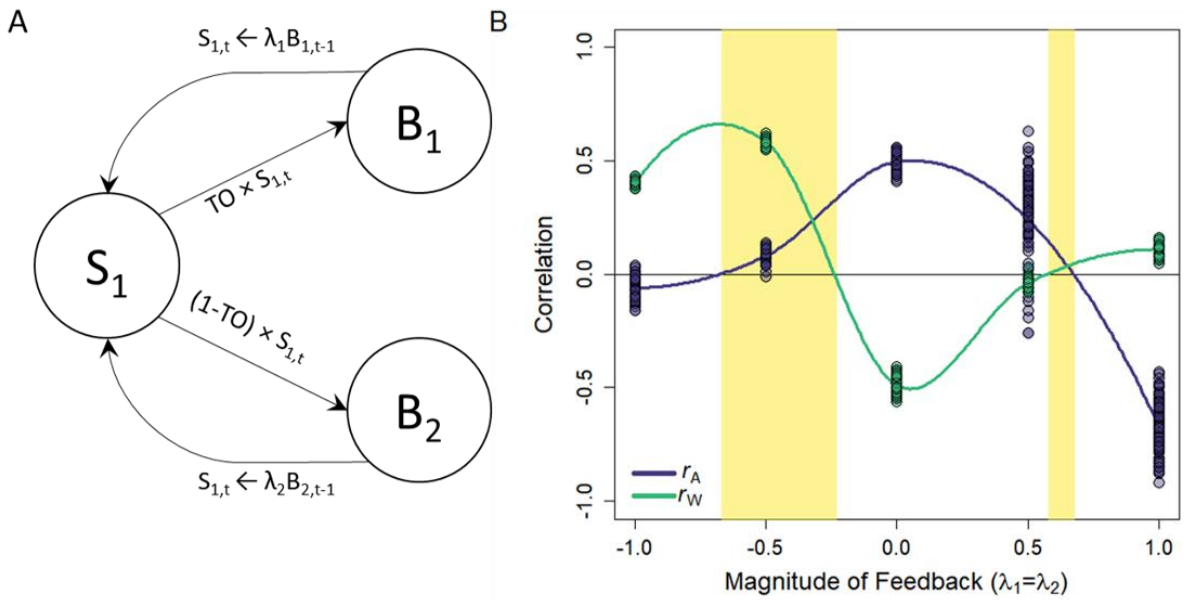

Figure 3. (A) Simple model structure combining Sih et al.'s (2015) feedback model with Houle's (1991) y-model to include feedbacks between behavior and state. TO (the trade-off parameter) is the proportion of state energy (S_1 at time t) allocated to behavior B_1, making 1-TO the energy allocated to B_2. λ is the feedback strength and the conversion rate of a behavior (B_1 or B_2) into energy that can be used at a later time. (B) Magnitude of among- (red) and within-individual (blue) correlations under feedbacks (λ) of different strength. Shaded regions indicate those feedback strengths that produce correlations of the same sign. Repeatability is not set *a priori* and is instead an emergent property of the model. Individuals within a population expressed behaviors according to A over ten time steps, with 250 individuals per population. Fifty populations were simulated at each of five levels of feebacks (λ in B). r_A and r_w were estimated using the `MCMCglmm` package in R (Hadfield 2010).

To determine whether feedbacks similarly produce both behavioral syndromes and integrated plasticity, I extended the Sih et al. (2015) model to two traits following Houle's (1991) classic y-model (Figure 3A). The y-model is a simple representation of trade-offs where "state" or some other proxy for energy (S_1) is allocated to expression of one of two traits (B_1 or B_2, Figure 3A). Because energy allocated to one trait at a particular time (TO × $S_{1,t}$) is not available for allocation to the other trait ((1-TO) × $S_{2,t}$), a trade-off exists between them.

Following this framework, I modeled the expression of two behaviors (B_1 and B_2) as emerging from the investment of energy (based on "state") into each, with the amount of

energy invested trading off between behaviors. In this model the two behaviors subsequently affect the gain of state/resources for use in the future expression of behavior via feedbacks (λ, the proportion of energy added back to S_1, Figure 3A). Biologically such feedbacks might arise if, for example, exploratory propensity is positively correlated with energy gain. In such a case, individuals with initially high state can explore more, gaining more energy that can be invested in even greater exploration and energy gain in the future—a positive feedback.

I modeled varied magnitudes of feedbacks and analyzed modeled populations to determine resulting among- and within-individual correlations (Figure 3B). At the start of the model, state differed among individuals due to stochastic variation. This seeded the population with variation in initial acquisition. In natural populations, individuals may similarly initially differ due to developmental stochasticity, parental investment, genetic differences, and other factors. If due to environmental variation, these individual differences are consistent with the generation of "pseudo-personality" (sensu Westneat et al. 2011).

In the absence of feedbacks ($\lambda_1 = \lambda_2 = 0$, Figure 3), this model reduces to the general structure of models developed by Houle (1991) and Van Noordwijk and de Jong (1986). Consequently, without feedbacks, the trade-off in allocation along with underlying variation in initial acquisition results in positive among-individual (r_A) and negative within-individual correlations (r_w, Figure 3B), i.e. negatively integrated plasticity and different signs for the two correlations. However, with both negative and positive feedbacks (negative and positive values of λ respectively), integrated plasticity becomes increasingly positive (Figure 3B). Simultaneously, negative and positive feedbacks lead to a reduction in

among-individual correlations, which become negative and trade-offs become particularly apparent at the among-individual level with strong positive feedback. Importantly, this model identifies both positive and negative feedbacks in two disjunct ranges that result in among-individual correlations and integrated plasticity of the same sign (shaded regions of Figure 3B). This suggests that feedbacks could partially explain the patterns of correlations observed in Figure 2.

The potential for state-behavior feedbacks combined with trade-offs to explain observed patterns of correlations adds to several prior models that suggested state can generate consistent individual differences and phenotypic behavioral correlations (Dall 2004, Wolf et al. 2007, Luttbeg and Sih 2010, Dall et al. 2012). However, these prior models did not separately examine among- and within-individual correlations nor the relationship between them.

Given that within-individual correlations more strongly influence observed correlations between behaviors than do behavioral syndromes, the mismatch in effort to understand these correlations over the last fifteen years has hindered our general understanding. While considerably more investigation is required, the simple model presented here suggests that feedbacks might play a role in shaping both behavioral syndromes and integrated plasticity. This potential for feedbacks to shape correlations can be empirically addressed via manipulation of food availability (e.g. MacGregor et al. 2021), manipulating population densities, and longitudinal measurements of both state and behavior (Sih et al. 2015). Regardless, whether focused on feedbacks or other potential causes, our understanding of behavioral correlations can only advance if more—and

100 careful—attention is paid to integrated plasticity and other contributors to within-

101 individual correlations.

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