Highlights and Perspectives on Evolutionary Neuroscience

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Flexibility and Constraint in the Evolution of Gene Expression and Behavior

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Central to understanding phenotypic evolvability is an understanding of the extent to which the mechanisms underlying a given phenotype are flexible versus constrained. Are there many possible mechanistic solutions for a given adaptive problem, or are biological systems constrained such that solutions are limited? Evidence that shared neural circuitry and molecular substrates (e.g., neuropeptides, hormones, signaling molecules) mediate similar behaviors exists across vertebrates [Striedter, 2005; O’Connell and Hofmann, 2011], and some studies argue for even more phylogenetically widespread conservation of mechanisms [Arendt and Nübler-Jung, 1996; Strasfeld and Hirth, 2013]. Contrasting these patterns of widespread overlap is evidence that distinct molecular mechanisms may generate similar phenotypes in closely related species, populations of the same species, or even among individuals in the same population [Crawford and Oleksia, 2007; Gaillard et al., 2009; Verster et al., 2014]. Evidence of distinct mechanisms mediating similar phenotypes suggests that multiple mechanistic solutions are possible and biological systems are indeed flexible. But what is the importance of mechanistic flexibility for the maintenance and evolution of biological systems?

Our understanding of how underlying mechanisms influence the evolvability of behavioral phenotypes remains limited. To shed light on this issue within the specific context of brains and behavior, I conducted three related studies that examined patterns of flexibility and constraint in the Trinidadian guppy, Poecilia reticulata. Guppies have become a model system in ecology and evolutionary biology due to their ability to rapidly adapt to novel environments. In Trinidad, guppies from high-predation sites have repeatedly and independently colonized low-predation environments, leading to parallel evolution in life history traits, morphology and behavior [reviewed in Magurran, 2005]. Moreover, we are able to tease apart genetic and environmental influences on adaptive phenotypes in the lab [Fischer et al., 2014].

Taking advantage of this unique system, my goal was to characterize forces facilitating and constraining behavioral evolution, and to explore interactions between developmental plasticity and evolutionary divergence in this context.

To explore patterns of flexibility and constraint at the level of behavior, I measured 21 behaviors across four assays and examined patterns of variation and covariation in behavior based on differences in evolutionary history with and lifetime exposure to predators (fig. 1). Contrary to classical predictions that trait correlations are stable across time and space [Lande, 1979; Schluter, 1996; Merilä and Björklund, 2004], I showed that behavioral correlations observed in one population or environment did not predict correlations in another and that environmentally induced flexibility in behavioral correlations shaped evolutionary trajectories. Recognition that trait correlations are flexible, even within the lifetime of an individual, will inform both theoretical predictions and empirical studies of adaptation.

Given evidence for flexibility at the level of behavior, I next asked how such flexibility manifested in underlying transcriptional mechanisms. My experimental design allowed me to link baseline differences in gene expression to multiple behavioral phenotypes and to connect variation in gene expression to variation in behavior.

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within and among groups (fig. 1). I observed alternative transcriptional states predicting behavioral differences across rearing environments and genetic backgrounds, despite a similar range of behavioral variation across these groups. These observations provide evidence for mechanistic flexibility by demonstrating that multiple underlying mechanisms (i.e. transcriptional states) can give rise to similar phenotypes (i.e. behaviors). The transcriptional changes I identified may represent either gene expression shifts that drive adaptive phenotypic differentiation or compensatory changes in gene expression that maintain phenotypes in the face of environmental change. In either case, flexibility at the transcriptional level may increase evolvability by balancing the maintenance of favorable trait constellations with the generation of phenotypic diversity during adaptation to novel environments.

Finally, I took advantage of parallel phenotypic evolution in guppies to compare gene expression signatures associated with adaptation across independent evolutionary lineages (fig. 1). I found evidence for both shared and distinct transcriptional mechanisms associated with parallel phenotypic evolution. Together with results from the first and second study, the findings of this third study suggest a potential role for mechanistic flexibility in increasing evolvability; alternative mechanisms for similar patterns of trait divergence may maintain cryptic variation that can be released and selected upon when environmental conditions change [Gibson and Dworkin, 2004; Schlichting, 2008; McGuigan and Sgrò, 2009].

In concert these studies demonstrate striking flexibility across behavioral phenotypes, behavioral mechanisms and repeated evolutionary events. Moreover, they suggest three ways in which flexibility may influence evolvability: (1) by enabling changes in trait correlations and
thereby reducing pleiotropic constraints imposed by these correlations, (2) by allowing compensatory transcriptional changes that maintain phenotypes in the face of environmental change and (3) by allowing underlying cryptic transcriptional variation that may facilitate adaptation under novel environmental conditions. Although our understanding of how differences in underlying mechanisms influence behavioral evolution is still limited, I propose that mechanistic flexibility increases evolvability. Guppies are known for rapid adaptation, and it remains to be seen whether the flexibility I observed is unique to rapidly adapting species or a fundamental principle governing how biological systems balance robustness and evolvability. Ultimately, a clearer description of mechanistic flexibility will promote our understanding of the forces limiting and potentiating adaptive evolution, and deepen our knowledge of how organisms respond to novel and changing environments.

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References

