A strong local dependency of developmental bias orients adaptive evolution in a model evo-devo system

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The differential production of phenotypes, that is, developmental bias, has been presumed to have a strong influence on the direction of evolutionary modification. In a computational evo-devo system generating neural connectivity, we demonstrate an orienting role for developmental bias during adaptive evolution. The differences in phenotypic transitions taken during evolution are, to a large degree, due to phenotypic accessibility being strongly dependent on the interactions of the developmental process as directed by a particular genotype. We define developmental bias as the differential production of phenotypes given uniform genetic variation. In our gene-based developmental system, we approximate the range of phenotypic variation possible by creating random genotypes and determining the phenotypes they produce. The resultant pattern of phenotypic variation indicates an intrinsic bias (global bias) in the developmental system. We then determine the accessibility of phenotypes from a given genotype (local bias) by determining the phenotypes generated through each and every single-base substitution. We find that the local bias patterns vary strongly with the genotype, even among phenotypically-neutral genotypes. These patterns also differ from the global bias pattern indicating local biases depend more on the dynamics of the developmental process than on the overall mechanisms of the developmental system.

During evolutionary simulations toward a target phenotype, the local dependency of bias dictates the phenotypic transformations that occur. For example, in two simulations at the generation preceding an increase in the populations' best fitness (the populations have approximately the same average fitness), the target phenotype is produced in one population but not in the other. The average of the local bias patterns for all individuals in the second population (population bias) shows the target phenotype is completely inaccessible through mutagenesis of the population. Other fitness-increasing phenotypic transitions show a similar result; the particular phenotype produced is dictated by the phenotypic variants accessible from the population. This results in multiple phenotypic pathways to the target phenotype across simulations.

Because local bias has such a strong dependency on the dynamics of the developmental process as determined by the regulatory structure of the genotype, bias patterns often change dramatically during evolution through the accumulation of mutations (neutral or otherwise). Phenotypic variants that are possible, as indicated by local bias patterns, occasionally are not able to be generated in subsequent generations. More importantly, phenotypes previously inaccessible often become available after multiple rounds of mutation. Mutations change the developmental context in which subsequent mutations operate. In one example, a mutation previously selectively-neutral eventually becomes a beneficial mutation, resulting in a change to a higher-fitness phenotype.

These results indicate that developmental bias has a strong influence on the direction of evolutionary modification. More generally, there are features of the genotype-to-phenotype and phenotype-to-fitness mappings that affect evolvability, the capacity to vary in phenotypic availability over time.