Bringing Back the Organism and Development

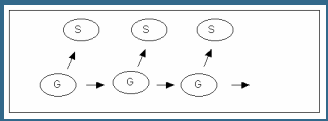
"all that we call phylogeny is to-day, and ever has been, ontogeny itself. Ontogeny is, then, the primary, the secondary, the universal fact. It is ontogeny from which we depart and ontogeny to which we return. Phylogeny is but a name for the lineal sequences of ontogeny, viewed from the historical standpoint" (Charles Otis Whitman, 1919, p. 178).

The Dismissal of Development

- "If there were to be a 'Modern Synthesis', there would have had to have been some 'Unmodern Synthesis' before it. This 'unmodern synthesis' was this union between embryology and evolution. The 'Modern' Synthesis would involve the supplanting of embryology by genetics, and one of Gregory Bateson's roles (in addition to naming the new field 'genetics') would be to destroy the notion that embryology contributed anything to our understanding of the mechanism of evolution." (Gilbert, p. 470).
- "Morphology having been explored in its minutest corners, we turned elsewhere...The geneticist is the successor of the morphologist." (Bateson, 1922)
- Development was largely excluded from the Evolutionary Synthesis

Doing Evolution without Development

- An organism is a collection of traits undergoing selection
- Each trait is an adaptation, constrained only by the constraints imposed by other adaptations
- Genes *code for/program* the traits of organisms
- We understand the traits of organisms by understanding the genes that code for them
- If we want to change traits, we need to change the genes



Enter the Adaptationist Perspective

- Darwin wanted to explain adaptations (traits that fitted their bearer to their local environment) and advanced natural selection as the answer
- What Gould and Lewontin call the "Adaptationist Programme" is the project of explaining traits as selected for an advantage they provided
  - Empirical claim: Most biological traits are adaptations
  - Explanatory project: Explain adaptive traits by natural selection
  - Methodological strategy: view traits as adaptations—optimal designs promoted by natural selection

Gould and Lewontin's Critique of Adaptationism

- Traits might be adaptive without being adaptations
- Traits can evolve without being adaptations
  - As consequences of other traits that are adaptive
  - As conserved traits due to existing *bauplan*
  - As product of developmental constraints
- Adaptationist explanations run the risk of being *just-so* stories
  - Typically are not subjected to rigorous tests
  - When found to be false, replaced with another

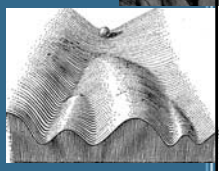
Spandrels of San Marco

- Spandrels are an inevitable consequence of mounting a dome on top of rounded arches
- Once spandrels existed, they became places on which to present art
- BUT, they were not included in the design as a place to put art

Gould and Lewontin's Alternatives

- *"attempt to reassert a competing notion (long popular in continental Europe) that organisms must be analyzed as integrated wholes, with baupläne so constrained by phyletic heritage, pathways of development, and general architecture that the constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs."*
- Non-selective means to new traits: pleiotropy, allometry, "material compensation," mechanically forced correlations (constraints)
- Constraints
  - Phyletic
  - Developmental and architectural

Canalization: C. H. Waddington



- State space of possible designs
- Development is a trajectory through such a space
- Options are limited
  - Once a given decision is made in the development of an organism, the range of state space to which it can go is constrained
- Development is *canalized*—it is limited to the options available in the particular canal it has entered
  - Allows for unrevealed variability
- Development constrains evolution:

Waddington: Development Constrains Evolution

- "Changes in genotypes only have ostensible effects in evolution if they bring with them alterations in the epigenetic processes by which phenotypes come into being; the kinds of change possible in the adult form of an animal are limited to the possible alterations in the epigenetic system by which it is produced."

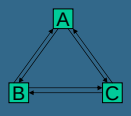
Waddington and Assimilation

- Phenotypic response becomes coded in genes. Four conditions for assimilation:
  1. The genome must be responsive to environmental inducers.
  2. The competence to be induced must be transferred from an external inducer to an internal, embryonic inducer.
  3. There has to be cryptic variation within a population so that the physiological induction can be taken over by embryonic inducers.
  4. There must be selection for the phenotype
- Sometimes called the *Baldwin Effect*
  - Captures a sense of *inheritance of acquired characteristics*

Kauffman's Puzzle

- One of the major discoveries of modern genetics is the complexity of genetic control: many genes don't code for traits, but regulate the expression of other genes
- Results in a highly complex network of genes
- What happens if the rate of mutation is even modest?
  - One might expect the results to be catastrophic

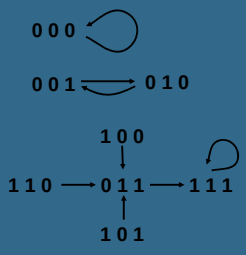
Kauffman's Boolean Attractor Networks



B	C	A
0	0	0
0	1	0
1	0	0
1	1	1

A	C	B
0	0	0
0	1	1
1	0	1
1	1	1

A	B	C
0	0	0
0	1	1
1	0	1
1	1	1



Model for genetic networks
- Only some variants are possible
- Selection is limited to stable configurations

Generative Entrenchment: William Wimsatt

Three designs for a lock

- Standard (no clues for any partial answers)
  - » .5 x 10^{10} = 5,000,000,000 tries to crack
- Cracker's delight (each wheel clicks when in the right position)
  - » 5 x 10 = 50 tries to crack

Ernst von Baer

- Developmental lock (Cracker's delight when solved from left to right, otherwise clicks are misleading)
  - » Wheels to the right are dependent on settings of wheels to the left
- In biological development: traits on which many others depend cannot be easily modified
  - » Early developmental stages are entrenched in evolution

Bringing Development Back

- The standard evolutionary synthesis picture views development as insignificant for understanding evolution
  - Development is the unfolding of the organism according to the program laid out in the genes
  - Any noise in the expression of genes does not affect the genes themselves
- Two alternative programs to standard view
  - Developmental Systems Theory (DST)
    - A radical theoretical/philosophical position
  - Evolutionary Development Biology (Evo-Devo)
    - A less radical emerging field in biology

Susan Oyama: Developmental Systems

- "If development is to reenter evolutionary theory, it should be development that integrates genes into organisms, and organisms into the many levels of the environment that enter into their ontogenetic construction" (p. 113).
- Developmental System:
  - "a mobile set of interacting influences and entities" comprising "all influences on development" at all levels, including the molecular, cellular, organismal, ecological, social and biogeographical (p. 72).

Genes Just Part of the Replicator Story

- Parity Thesis:
  - "any sense in which genes code for phenotypic traits, program development, or contain developmental information can be equally well applied to other factors required for development" (Griffiths and Gray, 2000)
- Intracellular resources required for development
  - Membranes to serve as templates for synthesizing new membranes from proteins
  - Mitochondria for energy
  - Chromatin marking system
  - Cytoplasmic chemical gradients

Genes Just Part of the Replicator Story - 2

- Extracellular resources required for development
  - Bush fires for eucalyptus trees
- But, according to orthodox Darwinism, these are not part of inheritance
- "In line with this theoretical role, developmental systems theory applies the concept of inheritance to any resource that is reliably present in successive generations, and is part of the explanation of why each generation resembles the last."
- Developmental system is a integrated system in which resources are made available to the developing organism

Niches: Found or Constructed?

- Traditional view is that a species' niche is just the environment it inhabits
  - The environment was there first and species find them and adapt to them
  - Environments do change, but the primary factors affecting it are not the species occupying it
- According to the Niche Construction view, niches are made, not found
  - Organisms alter their environment in ways that are better suited to themselves as well as adapting to these altered environments
- DST: the constructed niche is part of the what an organism inherits

Natural Selection and Developmental Systems

- A major emphasis in DST is on the stability of the developmental system, focusing on resources provided reliably to each new generation
- But there is also variability in developmental systems
  - Some developing systems may not be provided all the needed resources
  - Individual developing systems will show variability
    - Some developing systems may be particularly effective at extracting resources from their niche
    - Some developing systems will be particularly effective at providing resources to their offspring
    - Some developing systems will be particularly effective at constructing a niche suitable to them
- Natural selection operates on such developmental systems

Evolutionary-Developmental Biology (Evo-Devo)

- Bring development into the evolutionary story, but not by displacing the gene as the unit of inheritance
- Construe development as hierarchical, with emergence as higher levels
  - Processes at higher levels of organization involve non-linear interactions of components
    - Nucleus in tadpole intestinal cell interacts with environment and expresses itself as an intestinal cell
    - Transplant the nucleus to an enucleated frog egg, and it will participate in normal frog development
    - Common element—potential
- These non-linear interactions are important for the direction of evolution

Extragenetic Inheritance?

- Genes require an ovum to express themselves
  - Basic metabolism (mitochondria), protein synthesis, etc.
- To Evo-Devo, these are also products of genes—maternal genes
  - Two generational inheritance story
- DST sees inclusion of these entities as the opening to an extragenetic inheritance account