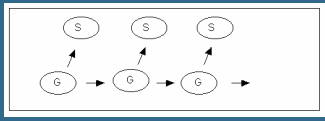
Bringing Back the Organism and Development

"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 Opponent: In Cartoon

- 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



The Claimed Primacy of the Gene

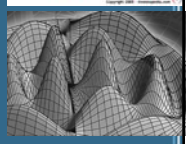
- In *The Selfish Gene* Richard Dawkins argues that genes alone replicate:
  - *The special status of genetic factors is deserved for one reason only: genetic factors replicate themselves, blemishes and all, but non-genetic factors do not.*
- Genes are replicators, organisms are only interactors
- Nature/nurture controversy
  - Often nature is equated with genetics, nurture with all the other influences on organisms

Adaptationism: Three stances

- Empirical adaptationism
  - Most biological traits are adaptations
    - Natural selection is the primary shaper of the traits of organisms
- Explanatory adaptationism
  - Apparent design is biology's central problem and natural selection is the fundamental answer
- Methodological adaptationism
  - As a strategy, view traits as adaptations—optimal designs promoted by natural selection

Optimizing and Game Theory

- Find the item amongst all the alternatives that optimally meets stated criteria
- Search the state space for the best solution
  - Search costs resources, so must factor in the cost of searching
  - Search until reach a maximum value of
    - Outcome – cost of searching
- Evolution interpreted as a search for optimal solutions
  - Generate many variants
  - Those that solve the problem best leave more offspring
  - Win the competition in the long-run



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

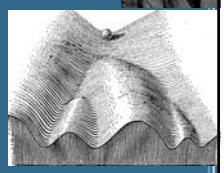
Gould and Lewontin's Alternatives

- *"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

Satisficing: Herbert Simon

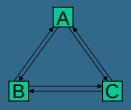
- Human rationality is bounded
- Set a criterion for a decision being "good enough"
- Search until an option is found that meets this criterion, then stop
- Apply to nature:
  - "It appears probable that, however adaptive the behavior of organisms in learning and choice situations, this adaptiveness falls far short of the ideal 'maximizing' postulated in economic theory. Evidently, organisms adapt well enough to 'satisfice'; they do not, in general, 'optimize'."

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

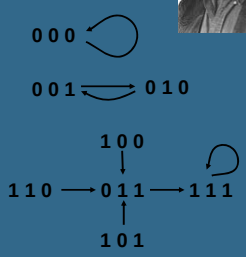
Boolean Attractor Networks: Stuart Kauffman



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

Generative Entrenchment: William Wimsatt

Three designs for a lock

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

Ernst von Baer

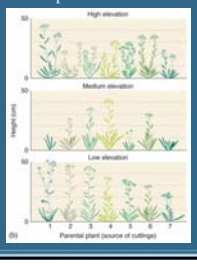
- Developmental lock (Cracker's delight when solved from left to right, otherwise clicks are misleading)
  - » Wheels to the right are dependent on settings of wheels to the left
- In biological development: traits on which many others depend cannot be easily modified
  - » Early developmental stages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

Genotype-Phenotype Complexity

- "If the mechanisms of development were such [that there was a one-to-one mappying of genotype and phenotype] the problem of understanding the manifest variation among organisms would then be reduced to providing a mechanical story of a chain of biochemical reactions, beginning with the reading of the genome by the cell and ending with the final state, much like the production of an automobile can be completely reconstructed from the blueprints, a description of the materials used, of the production machinery and of the order in which the materials pass through that machinery. However, the actual correspondence between genotype and phenotype is a many-many relation in which any given genotype corresponds to many different phenotypes and there are different genotypes corresponding to a given phenotype" (Lewontin)

Genotype-Phenotype Complexity - 2

- Many genetic changes can disrupt a protein
- Many traits require gene-gene interaction
  - Developmental canalization may buffer expression of genes
- Genes interact with environments in unpredictable ways
  - Same genotype tallest at high and low elevations, but not medium
- Purely stochastic effects
  - Asynchrony of cell division may have large down-stream consequences



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).

Robert et al.'s 7 Tenets of DST

Contextualism	Life cycles are contingent and contextually determined
Nonpreformationism	Hard : No ontogenetic information pre-exists individual ontogenies Soft: some ontogenetic information, though not exclusively genetic information, pre-exists individual ontogenies
Causal co-interactionism	Developmental causes interact in complex, often non-additive, ways
Causal dispersion	Causes of development are diffuse and fluid
Expanded pool of interactants	**Ontogeny is initiated and maintained by multiple entities and influences**
Extended inheritance	**A large set of heterogeneous ontogenetic resources and means are inherited**
Evolutionary developmental systems	**Evolution is change in the composition and distribution of developmental systems**

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
- 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 organisms 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

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