Adaptation, optimality, and function

Adaptive vs. Adaptation

- Traits are adaptive if they are beneficial to an organism in the here and now
- Traits are adaptations if they are the product of natural selection
  - They benefited the ancestors of the organism and figured in their selection
- All combinations are possible
  - Some traits are both adaptive and adaptations
  - Some traits are neither adaptive nor adaptations
  - Some traits are adaptive but not adaptations
  - Some traits are not adaptive but adaptations

Biological niches change

- Traits that were adaptive may cease to be
  - Vestigial organs such as the appendix
- Traits that were adaptations may come to serve a different adaptive role
  - Preadaptations or exaptations

Teleology and functions

- For Aristotle, natural phenomena were teleological
  - Events happened *to* produce results
- The scientific revolution seemed to remove purpose from the world
  - Events happened solely because of prior causes
- But teleological talk is preserved in the language of functions
  - The heart's function is to pump the blood
  - The kidney's function is to filter and remove waste
  - The function of the ribosome is to synthesize proteins

Functions and natural selection

- One strategy: explain the function of something in terms of what it was selected for
  - Treat it as an adaptation
  - Function explained etiologically
- Another strategy: explain the function of something in terms of what role it is playing today
  - Treat it as adaptive
  - Function treated as a propensity
- Third alternative: explain the function in terms of the contribution something makes to an operating system
  - Detach function from natural selection
  - Function in terms of contributions to the operations of a mechanism

When is a trait an adaptation?

- To be an adaptation, a trait must have figured in the reproductive success of ancestors, thereby providing an explanation of the presence of the trait in current organisms

- How common are adaptations?
  - Adaptationism: the default assumption when identifying a trait is that it is an adaptation to some selection forces
    - Heuristic for evolutionary biology—find the selection forces which selected the trait and made it an adaptation
 - Alternative: only some traits are adaptations

Adaptationism: Three accounts

- 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

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

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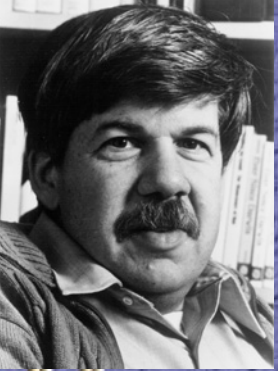
Gould and Lewontin's Critique of Adaptationism

- 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 empirically vindicated

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

Satisficing: Herbert Simon
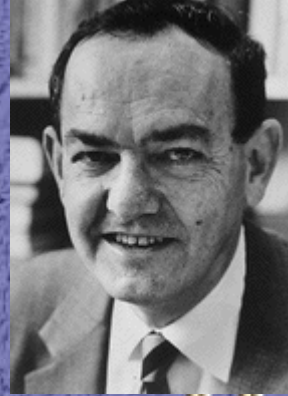
- Human rationality is bounded
- Set a criterion for a decision being "good enough"
- Search until an option is found that meets this criteria, then stop
- Apply to nature:
  - "It appears probable that, however adaptive the behavior of organisms in learning and choice situations, this adaptiveness falls 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
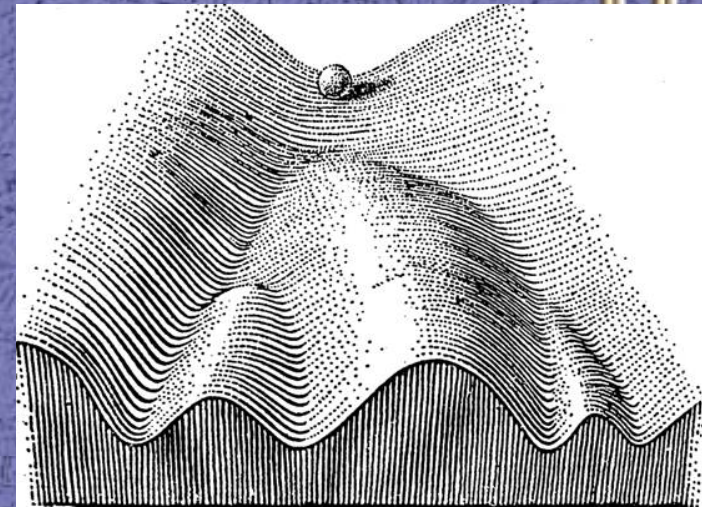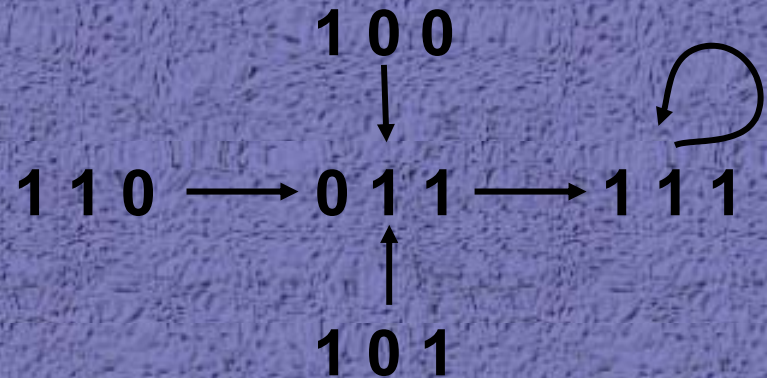
Boolean Attractor Networks: Stuart Kauffman
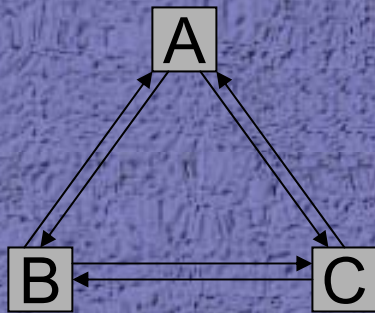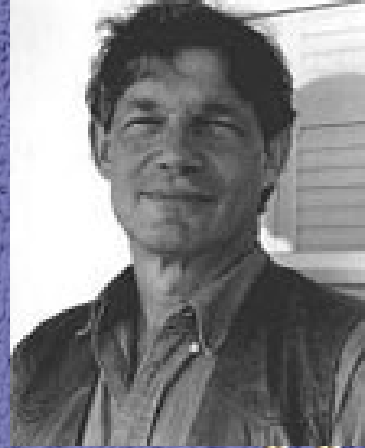
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0	1	0
1	0	0
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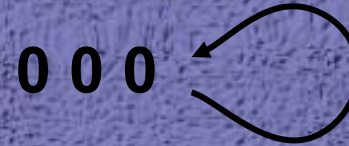
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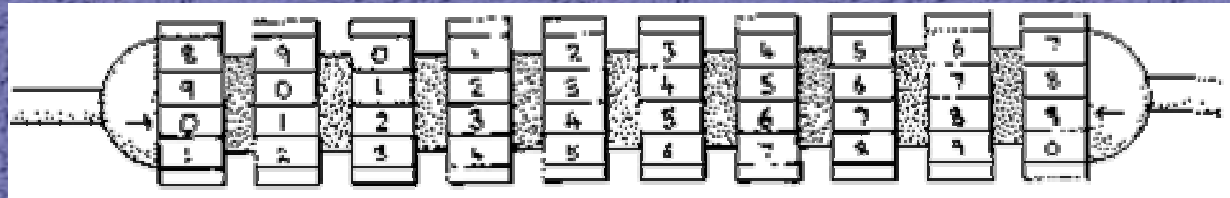| A	B	C
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1	0	1
1	1	1

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)
  - $5 \times 10 = 50$ tries to crack

- 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

Ernst von Baer

Testing for adaptations

- Even if the critics of adaptationism are right, there are adaptations
- Challenge: how to test the claim that a trait is an adaptation
  - Both the selection forces and alternative traits are usually hypothesized
  - Seek best explanation for the observed phenomena
    - Problem: to many free parameters
      - Can always fit the phenomena
- Using the comparative method to achieve further constraint

Comparative Method

- Comparisons with other branches in the phylogenetic tree can provide evidence regarding a claims as to what has been selected (and so is an adaptation
- Do the proposed selection events fit the phylogenetic pattern?
  - If two alternatives (one vs. two horned rhinoceroses) are both evolutionarily stable strategies, then neither can be invaded by the other
    - But the one-horned species evolved from the two-horned one
- Are there regular relationships between changes in traits and changes in habitat in a lineage?