

Evolution in Four Dimensions

Chapters 4-6

Outline by John Protevi of

Eva Jablonka and Marion Lamb, *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life* (MIT, 2005)

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Interlude: Transition to Part II

- I) Two problems
 - A) Genetic system is thought to be sufficient
 - B) Properties of genetic system are attributed to other systems
- II) Analogy: genotype = score; phenotype = performance
 - A) Transmission:
 - 1) Transmission of genotype: copying
 - 2) Transmission of phenotype: reproduction of interpretations of score
 - B) Direction of effect
 - 1) Usually only changes in score affect performance
 - 2) But sometimes changes in performance (phenotype) affects score (genotype)
 - C) Consequences
 - 1) Transmission systems have different technologies
 - 2) Other systems complement but do not replace genetic system
 - 3) Phenotypic variation / evolution can proceed independent of genetic change

Chapter 4: Epigenetic Inheritance System (EIS)

- I) Cell differentiation must have a memory system, not just a genetic triggering system
- II) Thought experiment: evolution via EIS w/o any genetic change: asexual reproduction
 - A) Double role of EISs allows for "directed or interpretive variation"
 - 1) Response system
 - 2) Transmission system
 - B) Discussion of thought experiment
 - 1) Different use of same DNA: regulation of gene expression
 - 2) Variants w/in each network of regulation of gene expression
 - a) NB: *not* a "regulatory gene network"
 - b) Bcs that implies it's only genes that do the regulating
 - c) Rather it's the distributed cellular system that regulates gene expression
 - 3) EIS transmit

- a) Interpretations of DNA information
 - b) Phenotypes rather than genotypes
- III) Four types of EIS (all of which work together and interact: see p. 137)
- A) Self-sustaining loops: memories of gene activity
 - 1) Stability / instability
 - a) Simple loops can switch easily to alternate states (small threshold for perturbation)
 - b) Complex loops can be resilient / stable (large threshold for perturbation)
 - 2) Type of information
 - a) Loop is unit of heritable variation, so information is "holistic" / nondecomposable
 - b) Versus the modularity of DNA
 - 3) Amount of variation depends on number of interacting loops
 - a) A single isolated loop has two state: on or off
 - b) But with networks of loops we have lots of permutations / variation
 - B) Structural inheritance: architectural memories: cell structures
 - 1) Ciliates: templates: variation in organization, not components
 - 2) Cavalier-Smith and the "membranome" in early evolution
 - a) First true cells
 - b) Bacterial groups
 - c) Eukaryotic cell
 - 3) Prions: self-templating proteins:
 - a) Diseases: kuru / CJD / BSE
 - b) Adaptive roles in multicellulars?
 - 4) Information and replication
 - a) Holistic information
 - b) No special / content-insensitive replication: only specific reconstruction
 - C) Chromatin marking systems: chromosomal memories
 - 1) DNA is tightly wound via "chromatin packaging"
 - 2) Chromatin marks allow inheritance of pattern of gene expression
 - a) DNA methylation
 - i) Do not affect protein coding, but only regulatory sites, hence probability of transcription
 - ii) Part of heredity system transmitting epigenetic info in cell lineage
 - (a) Hitchhike on DNA replication during mitosis (= somatic cell lineages)
 - (b) But what about meiosis (= generation of gametes)?
 - iii) Content-insensitive copying / modular information
 - b) Protein complexes
 - c) Histone marks
 - D) RNA interference: Silencing of the Genes
 - 1) Complex mechanism
 - 2) Basic idea: part of cellular genomic immune system
 - 3) Variations can have big developmental effects
- IV) Examples of Epigenetic inheritance
- A) Controversy: EIS between generations, not just in somatic cell lineages? (see W-E review)
 - 1) Single celled eukaryotes: all 4 mechanisms in

- 2) Bacteria: Methylation marks
- 3) Multicellulars:
 - a) Asexual reproducers: no theoretical problem for X-gen EIS
 - b) Sexual reproducers: Fertilized egg must allow cell differentiation, so it must be neutral
 - i) So it was assumed epigenetic history was wiped clean before gamete production
 - ii) So "parental genomic imprinting" was big surprise:
 - (a) Different sexes produce different chromatin marks
 - (b) But these are transient: erased when chromosome passes to other sex
 - (c) So it doesn't seem good candidate for evolution
- B) Examples of persistent X-gen EIS
 - 1) Methylation
 - a) Silencing of transgene by inherited heavy methylation
 - b) Modification of patterns of ordinary gene activity:
 - i) Peloric plants: stable and transmitted "epimutation": different methylation of a gene
 - ii) Yellow mice: variation in methylation pattern on extra DNA from transposon
 - 2) What about X-gen EIS by RNA interference?
- C) Conclusion
 - 1) EIS = another source of variation = another dimension of evolution
 - 2) Epigenetic variation (EV) vs genetic variation
 - a) Occurs much faster, especially under changed environment
 - b) Several EVs may occur at same time
 - c) May not be blind to function, and hence increases chance of adaptive variation
 - 3) Role in speciation?
 - 4) EIS not just cellular: e.g., uterine environment among Mongolian gerbils
- V) Dialogue
 - 1) Non-DNA heredity may have preceded DNA system
 - 2) Why include all 4 systems together? They all transmit "information"
 - 3) These systems seem more developmental than evolutionary
 - a) These systems are both heredity and regulatory systems
 - b) Thus evo / devo / physio are linked
 - 4) Organism level advantages are needed from evolution (target of selection)
 - 5) Epigenetic variants passed to gametes?
 - a) Variant somatic cells can develop into gametes
 - b) Information exchange between somatic cells and germ line (RNA interference)
 - 6) Variant somatic cell types as basis for X-gen development?
 - a) Gametes must have full developmental (cell differentiation) potential
 - b) But this doesn't exclude chromosome marks in egg that bias only some development
 - 7) Cloning uses [already differentiated] somatic cells
 - a) Their specialization must be erased to allow full cell differentiation
 - b) Don't forget there are a lot of developmental errors in cloning
 - 8) Reliability of epigenetic inheritance
 - a) Admittedly less than for genetic variations
 - b) But this low reliability can be supplemented by stable environmental induction
 - 9) What exactly is transmitted by EIS?

- a) P. 151: "components of an activity or a state that biases the reconstruction of same activity or state in next generation."
 - b) Thus we have to think in terms of reconstruction rather than copying (Very Important!)
 - i) Most likely with chromatin marks or RNA interference
 - ii) Other routes between soma and germ line: aren't they contra the central dogma?
 - (a) No, CD only forbids info from protein to DNA / RNA (reverse translation)
 - (b) Going from RNA to DNA (reverse transcription) is not a problem
 - (c) Info bypassing germ line (e.g., substances in mother's milk) is no problem
- 10) No direct evidence of adaptive X-gen epigenetic variation

Chapter 5: Behavioral Inheritance Systems (BIS)

- I) Thought experiment: evolution via BIS w/o genetic or epigenetic change
 - A) Info must be transmitted and acquired so that behavior is reconstructed
 - B) Culture = "system of socially transmitted patterns of behavior, preferences, and products of animal activities that characterize a group of social animals"
 - C) Cultural evolution = "change, through time, in nature and frequency of socially transmitted preferences, patterns, or products of behavior in a population"
 - 1) Mostly independent of genetic evolution
 - 2) But the two systems can intersect
- II) Transmitting information through social learning: 3 forms of BIS
 - A) Transfer of behavior-influencing substances
 - 1) Means of transmittal
 - a) Uterine environment
 - b) Milk
 - c) Saliva / breath
 - d) Feces
 - 2) Enables avoidance of trial-and-error learning
 - 3) Information
 - a) Holistic
 - b) Transferred substance is building block enabling reconstruction of mother's behavior
 - 4) Two further properties
 - a) Non-parental transfer is possible (adoption)
 - b) Usually non-blind variation:
 - i) Info via acquisition and testing by mother
 - ii) Variations due to her development and learning
 - B) Non-imitative learning: observation allowing reconstruction
 - 1) Non-material information transfer: requires interpretation by recipient
 - 2) Imprinting: usually there is a relatively early window for learning
 - a) Behavioral imprinting
 - b) Sexual imprinting
 - 3) Attention is drawn to features of environment / outcome of behavior (goal, not method)
 - 4) Information:
 - a) Must be displayed (no latent info, as with genetic system)

- b) Holistic
 - c) Never a random or blind variation (requires interpretation / reconstruction)
 - d) Not limited to parental transmission
 - e) Not many variants concerning any one behavior
- C) Imitative learning
- 1) E.g., vocal imitation, as in birds, whales, dolphins
 - 2) Information
 - a) Must be displayed
 - b) Modular, not holistic
 - 3) Variants not blind to function
 - a) Needs "internal filter" to identify potentially useful variants
 - b) Variations are targeted and culturally constructed
 - i) Simple rules to organize perceptions, emotions, learning (categories)
 - ii) Type of info is structured by evolutionary history of its lineage
 - 4) Recipients play active role:
 - a) "niche construction": animal activity changes environment / selection pressures
 - b) So one generation's actions in constructing a niche will bias info transmission / reception
- III) Traditions and cumulative evolution: evolving new lifestyles
- A) Obviously, we have to consider genetic basis of capacity for culture
 - B) There's no basis for assuming animal culture is limited in scope / complexity
 - 1) There hasn't been a lot of research done here
 - 2) Question of funding
 - a) Molecular biology / biotech / corporation / grants system
 - b) Basic research vs applied research
 - c) Bayh-Dole Act and shift to "public-private partnerships" in biotech research
 - d) Public funding of infrastructure ("risk")
 - i) Buildings
 - ii) Education
 - e) Private appropriation of success ("profit")
 - C) Evidence of cumulative cultural evolution among nonhuman animals: Japanese beach monkeys
- IV) Dialogue
- A) Early experience is important, but not absolutely determining
 - B) Genetic predispositions vs learned preferences
 - 1) Probably no visible difference in behavior
 - 2) X-gen effects
 - a) Genetic info can be latent: it is passed on even w/o environmental inputs
 - b) Learned preferences only transmitted w/ environmental input
 - i) Thus the preference can easily die out
 - ii) What can account for cultural tradition then?
 - (a) Need stable environment for continued tradition (i.e., transmission of variants)
 - 1. This can lead to "environmental addiction"
 - 2. And degradation of genes for that preference
 - a. This is called "masking": stable environment hides genetic variation
 - b. IOW, you get successful phenotype even w/ degraded genome

- (b) And / or variant is stabilized by links to other behaviors and / or environment
- C) Targeted variations can be stabilized by "functional fidelity"
 - 1) With genes, you need highly reliable replication of structural genes to conserve adaptations
 - 2) But with other inheritance systems, you just need whatever works:
 - a) "content" doesn't need to be the same
 - b) Effects just need to be as good or better
- D) Role of BIS in speciation
- E) Altruism and NS
- F) Horizontal transmission allows for bad behaviors to spread
- G) Animals are not passive recipients of BIS!
- H) Inseparability of heredity / evolution and development
- I) Insect traditions?

Chapter 6: Symbolic Inheritance System (SIS)

- I) Intro: discussion of symbols as key to human uniqueness
- II) Thought experiment: Crusoe and the parrots
 - A) Similarities of parrot calls and human language
 - 1) Signs are arbitrary
 - 2) Signs are referential
 - 3) Signs are conventional
 - B) Differences between parrot calls and human language
 - 1) Parrots have poor repertoire
 - 2) Sign system is rigid; each sign is a unit
 - a) They don't generalize the properties of words and apply to new items
 - b) They don't grasp relation between words
 - C) Humans: words are symbols bcs part of rule-governed system of self-referential signs
 - 1) Can transfer truth-value, emotional value and action value to sentence level
 - 2) Can not only go from situations to words, but from word combinations to situations
 - 3) Rule-bound generation of variants
 - D) General properties of symbols
 - 1) Interpreted w/in shared cultural framework of practices w/in which symbols function
 - 2) Meaning of symbols depends on
 - a) Relations of symbols to way culture experiences objects / actions in world
 - b) Relations of symbols to other signs in the cultural system
 - 3) Thus we have a "shared imagined reality"
 - E) JP: I would add that this treatment underplays the affective dimension:
 - 1) Cultural practices teaching meaning of symbols w/in a system
 - 2) Also shape the affective aspect of the "body politic"
 - a) Patterns, triggers, thresholds of basic and social emotions
 - b) This historically developed body politic is what generates moral intuitions
- III) Symbolic communication as inheritance system
 - A) Shared structure w/ genetic system: transmission of latent information
 - B) Difference from genetic system: unlimited translatability into different media

- C) New symbolic information is targeted
 - 1) Fit with tradition
 - 2) With an eye to innovation and readiness for future
- D) Structure
 - 1) Language is modular
 - 2) Picture / dance tends to holism, but retains some modularity
 - 3) Hierarchical organization
- E) Many transmission paths: vertical and horizontal
- F) Requires active instruction
- IV) Cultural evolution and symbolic communication
 - A) Symbols permeate all aspects of human culture
 - 1) Even acquired behaviors have symbolic association
 - 2) JP: as do practices forming "body politic" / affective cognition
 - B) Many cultural evolution models are problematic
 - 1) They assume copying vs reconstruction (= active acquisition / interpretation)
 - 2) JP: for me, "information" is problematic too
 - a) Even if reconstructed, rather than copied
 - b) I'd rather focus on affective cognition / body politic formation
- V) Competing Theories
 - A) "Selfish Memes"
 - 1) Presuppositions:
 - a) Meme = unit of information embodied in neural circuits
 - b) Relies on memes as replicators and organism – cultural products as vehicles
 - 2) Criticisms:
 - a) Vehicles cannot transmit acquired variations
 - b) But heritable variation in behavior and ideas (allegedly, "memes")
 - i) Are reconstructed (by the alleged "vehicles") in next generation's development
 - ii) Hence can transmit variations, bcs learning is function / meaning sensitive process
 - c) Reconstruction of a behavior ties together transmission and the transmitted variant
 - i) The developmental consequence (= neural circuits for the behavior)
 - ii) Come not by copying but by reconstruction of a social / environmental network
 - (a) So transmission is not simply copying of the transmitted unit
 - (b) But is a property of a distributed system
 - B) Evolutionary psychology (EP) and mental modules
 - 1) JP: Preliminary distinction (not offered by authors)
 - a) Sociobiology: explananda = behaviors
 - b) EP: explananda = psychological modules producing tendencies for behavior
 - 2) Characteristics of EP
 - a) Gene-centered: culture is veneer
 - b) Massive modularity of mind / embodied in specific neural networks
 - c) Selection during Pleistocene
 - d) Possible contemporary mal-adaptivity of inherited module (which *was* an adaptation)
 - 3) Alternate explanations
 - a) Neural plasticity (especially in cortex)

- i) Thus I can accommodate some modules, esp. for basic emotions
 - ii) But deny "massive" modularity, esp. for complex social situations
 - b) Culture as productive
 - i) Culture is not simply a modification of underlying structure
 - ii) IOW, cultural practices produce body politic via neural plasticity
 - (a) Cultural differences cannot be decoded to reveal universal human nature (UHN)
 - (b) I believe in such a UHN (I'm not a pure social constructivist)
 - 1. But UHN is limited to patterns basic emotions
 - 2. While triggers and thresholds are plastic and constructed by culture
 - 4) Thought experiment: "literacy module"
 - a) Evidentiary issues:
 - i) Reasons to be tempted to posit evolved literacy module
 - (a) Complex behavior
 - (b) Yet easily acquired at early age by almost every child
 - (c) And disrupted by neurological anomalies
 - ii) Can also be explained by combination of two factors
 - (a) Pre-existing cognitive adaptations
 - 1. But not for "literacy"!
 - 2. But for pattern recognition, etc.
 - (b) Wide spread and continuously reproduced environmental inducers
 - 5) Methodological issues with EP
 - a) No neurological data to back up EP (on the contrary, cortical plasticity is rule)
 - b) EP relies on inferences from psychological tests
 - c) Overlooking of more plausible cultural explanations
 - i) E.g., sexual selection argument for greater male creativity
 - ii) Parsimony of explanation would argue for cultural explanation
 - 6) Major difficulties with central planks EP
 - a) Universality and invariance
 - i) Explanation by means of gene-based psychological module
 - ii) May be premature bcs social universals haven't been identified
 - b) Ease of acquisition (Chomsky vs Deacon)
 - i) Chomsky: poor quality input but impressive competence anyway = language organ
 - ii) Deacon: coevolution of language and neural capacities = ease of learning
 - (a) Cultural evolution can adapt to capacities of brain
 - (b) Cultural niches can then exert selection pressure on brain
- VI) From evolution to history
- A) EP and memetics are Darwinian:
 - 1) Cultural competition is only a selection factor for mysteriously generated variations
 - 2) Which are quite strongly constrained by inherited modules anyway
 - B) JL are Lamarckians:
 - 1) Culture also generates directed variation via capacity for future planning
 - 2) And culture operates so as to consolidate and create mutually reinforcing life-styles
 - a) Thus it's impossible to isolate a "meme" or "module" for independent selection
 - b) Because "selection, generation and transmission" of cultural variants

- i) Are linked together
- ii) And embedded in economic, legal and political systems

C) Example of change in punishment for stealing sheep

VII) Dialogue

A) Relation of language to other symbolic systems

- 1) Language transformed gesture into symbolic system
- 2) Language co-evolved with other symbolic modes (Merlin Donald)

B) Culture as emergent

- 1) Are cultural products autonomous replicators merely inhabiting robotic vehicles
- 2) No; even though culture is independent of any one individual, humans are agents
 - a) "Men make history, but not on conditions of their own choosing"
 - b) Need to see diachronic and not just synchronic emergence
 - i) Synchronic: part / whole leads to impossible problems
 - (a) Individual / society
 - (b) Structure / agency
 - ii) Diachronic:
 - (a) Highlights issues of X-gen reconstruction
 - (b) And criteria for identifying "crisis zones / periods" for innovation

C) Latent cultural information can be transmitted: potential for variants to be created later

D) Is "cultural evolution" really a useful term?

- 1) Can you give a rigorous definition?
- 2) Why not just give thick descriptions of cultures (Geertz)?
- 3) David Hull's definition of Lamarckianism vs Mayr and "soft inheritance"

E) EP and UHN

F) JL's final statement: agency and the "tangle of construction"