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
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 eukayrotes: 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 a 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 a 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"