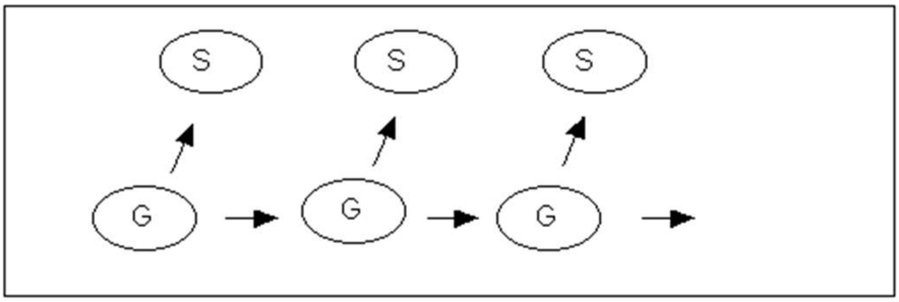
Development and evolution

The place of culture in Evolution

- The place of culture in Evolutionary Psychology
- The place of culture in Ethology / in Primatology
- The place of culture in Evolutionary Biology

Germline x Somatic cells:

the “Weismann barrier”



Ontogenetic development in the ethological approach

J. Huxley 1942: Behavior:

Adaptive Function

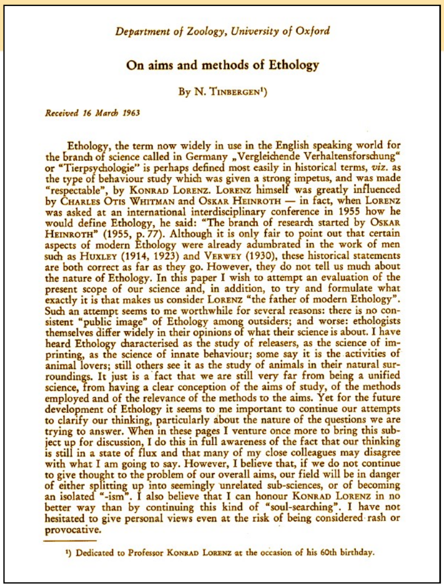
Immediate Causation

Evolutionary history

Tinbergen 1963:
the “4 Questions”:

+ ONTOGENY

Instinct & learning



Department of Zoology, University of Oxford

On aims and methods of Ethology

By N. TINBERGEN[1])

Received 16 March 1963

Ethology, the term now widely in use in the English speaking world for the branch of science called in Germany „Vergleichende Verhaltensforschung“ or “Tierpsychologie” is perhaps defined most easily in historical terms, *viz.* as the type of behaviour study which was given a strong impetus, and was made “respectable”, by KONRAD LORENZ. LORENZ himself was greatly influenced by CHARLES OTIS WHITMAN and OSKAR HEINROTH — in fact, when LORENZ was asked at an international interdisciplinary conference in 1955 how he would define Ethology, he said: “The branch of research started by OSKAR HEINROTH” (1955, p. 77). Although it is only fair to point out that certain aspects of modern Ethology were already adumbrated in the work of men such as HUXLEY (1914, 1923) and VERWEY (1930), these historical statements are both correct as far as they go. However, they do not tell us much about the nature of Ethology. In this paper I wish to attempt an evaluation of the present scope of our science and, in addition, to try and formulate what exactly it is that makes us consider LORENZ “the father of modern Ethology”. Such an attempt seems to me worthwhile for several reasons: there is no consistent “public image” of Ethology among outsiders; and worse: ethologists themselves differ widely in their opinions of what their science is about. I have heard Ethology characterised as the study of releasers, as the science of imprinting, as the science of innate behaviour; some say it is the activities of animal lovers; still others see it as the study of animals in their natural surroundings. It just is a fact that we are still very far from being a unified science, from having a clear conception of the aims of study, of the methods employed and of the relevance of the methods to the aims. Yet for the future development of Ethology it seems to me important to continue our attempts to clarify our thinking, particularly about the nature of the questions we are trying to answer. When in these pages I venture once more to bring this subject up for discussion, I do this in full awareness of the fact that our thinking is still in a state of flux and that many of my close colleagues may disagree with what I am going to say. However, I believe that, if we do not continue to give thought to the problem of our overall aims, our field will be in danger of either splitting up into seemingly unrelated sub-sciences, or of becoming an isolated “-ism”. I also believe that I can honour KONRAD LORENZ in no better way than by continuing this kind of “soul-searching”. I have not hesitated to give personal views even at the risk of being considered rash or provocative.

[1]) Dedicated to Professor KONRAD LORENZ at the occasion of his 60th birthday.

Is Evolutionary Psychology a metatheory for psychology? Ploeger et al 2008

Evolutionary Psychology
+ Developmental Evolutionary Biology?

Evolution, behavior , and "life history":
Development as the target of Natural Selection

Heterochronies: neoteny (pedomorphism) and human evolution

Criticism: Neo-Darwinian Synthesis "contempt" for development

Is Evolutionary Psychology a metatheory for psychology? Ploeger et al 2008

Neo-Darwinian theory: only a change in genetic structure can be the initiator of evolutionary change.

Evolutionary developmental biology: new variants emerge before natural selection can do its work. The relevance of natural selection is not disputed, but individual development and behavior can be viewed as the initiator of evolutionary change: developmental change leads to new behavior, which may be better suited to certain environmental conditions. The new behavior brings out latent possibilities for physiological or morphological change. The issue is whether the original change in behavior requires a genetic mutation.

Is Evolutionary Psychology a metatheory for psychology? Ploeger et al 2008

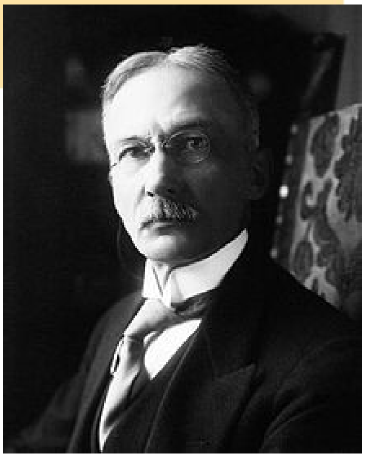
Gottlieb (2002, 2003): **evolution of the apple maggot fly**: a genetic mutation is not required to produce new behavior. Originally, the female apple maggot fly laid her eggs on hawthorns. When domestic apple trees were introduced, females started to lay their eggs on these as well (phenotypic change). Now, there are 2 variants of the apple maggot fly, one that lays its eggs on apples and the other on haws. They no longer mate with each other: apples mature earlier than haws (so mating seasons are different). This change in developmental timing has given rise to genetic changes in the two populations (Feder et al 1997).

Is Evolutionary Psychology a metatheory for psychology? Ploeger et al 2008

Note (...) the clear difference with Lamarckian theory, which states that acquired characteristics are transmitted biologically to the offspring.

The evolutionary developmental point of view is that new behaviors (phenotypic changes) create new possibilities to deal with environmental conditions, which set the stage for later genetic change.

The "Baldwin effect"


James Mark Baldwin (1861 - 1934)

Epigenetic factors and evolution

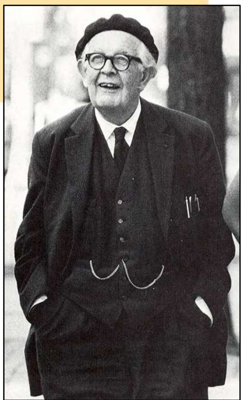
Phenotypic variability
(ex: new, learned behaviors)
affects genetic inheritance
(not only Natural Selection).

Baldwin x Lamarck

Human behavior: culture and genetic evolution
(ex: Incest taboo: if powerfully enforced, removes the natural selection pressure against the possession of incest-favoring instincts)

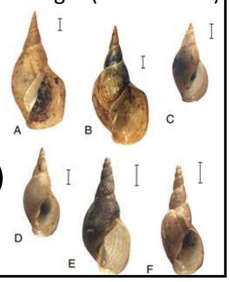
Human migrations (Out of Africa & beyond)

Baldwin & Piaget


Jean Piaget (1896 - 1980)

"Circular reaction":
Assimilation and Accommodation

If the environment never changes, then the organism is born equilibrated; the inherited evolutionary history of the species has shaped its individual fitness, into which it must simply mature. But if the environment does change, then the organism must respond if it is to stay equilibrated: first it must assimilate the effects of the change, then it must accommodate its way of life to that change in order to retain its fitness (Burman 2012)



J. Piaget: mollusk shells (*Lymnaea*)

Evolution in Four Dimensions
Jablonka & Lamb 2005, 2007

"Darwin's laws were very general. How **reproduction**, **growth**, and **inheritance** are realized in different biological systems, how **variability** is generated, and what types of competitive interactions are important, all had to be qualified. Evolutionary biology since Darwin can be seen as the history of the qualification of these processes."

"August Weismann gave natural selection an exclusive role in evolution, ruling out change through the inherited effects of use and disuse or any other form of the inheritance of acquired somatic characters. **Sharp distinction between cells of the soma, which are responsible for individual life, and germline cells, which are responsible for producing sperm and eggs**."

Evolution in Four Dimensions
Jablonka & Lamb 2005

Weismann (1890): meiosis
Johannsen (1911): genotype and phenotype.

"One thing that most mid- and late-20th century evolutionists were unwilling to incorporate into their theory was the possibility that the **generation of new variations might be influenced by environmental conditions**, and, hence, that not all inherited variation is "random" in origin. During the first 50 years of the Modern Synthesis's reign, **Lamarckian processes**, through which influences on development could lead to new heritable variation, were assumed to be non-existent."

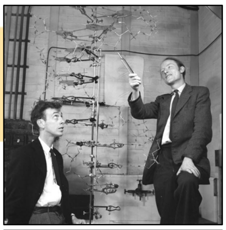
Developmental processes in general were not a part of the Modern Synthesis.

Evolution in Four Dimensions
Jablonka & Lamb 2005

The Modern Neo-Darwinian Synthesis” (late 1930s)
Ideas and information from paleontology, systematics, studies of natural and laboratory populations, and especially, from genetics, were integrated into the neo-Darwinian framework.

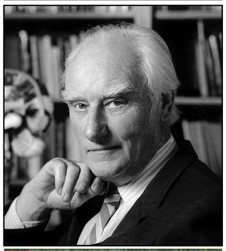
(1) **Heredity takes place through the transmission of germline genes**, which are discrete and stable units located on nuclear chromosomes. They carry information about characters.
(2) **Variation is the consequence of the many random combinations of alleles generated by sexual processes**; usually, each allele has only a small phenotypic effect.
(3) **New alleles arise only through accidental mutations; genes are unaffected by the developmental history of the organism**, and **changes in them are not specifically induced by the environment**, although the overall rate of change might be affected.
(4) **Natural selection occurs between individuals** (although selection between groups was not explicitly ruled out).

The double Helix



Crick & Watson (1953): **DNA** structure

Molecular biology (1950s): According to Francis Crick's central dogma, information can never flow from a protein back to RNA or DNA sequences, so developmental alterations in proteins cannot be inherited.

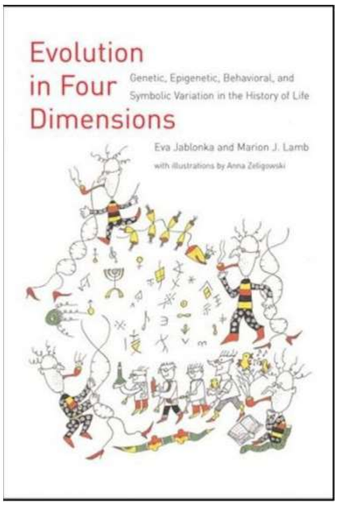


Dawkins 1976 (The Selfish Gene): Even greater focus on the gene not only as a unit of heritable variation, but also as a unit of selection.

Evolution in Four Dimensions
Jablonka & Lamb 2005

Four types of inheritance:

- Genetic
- (Cellular) Epigenetic
- Behavioral
- Symbol-based



Epigenetic inheritance

Epigenetic inheritance in the broad sense is the **inheritance of phenotypic variations that do not stem from differences in DNA sequence**. This includes cellular inheritance, and body-to-body information transfer that is based on interactions between groups of cells, between systems, and between individuals, rather than on germline transmission.

Body-to-body transmission takes place through developmental interactions between mother and embryo, through social learning, and through symbolic communication.

Cellular epigenetic inheritance is the transmission from mother cell to daughter cell of variations that are not the result of DNA differences. It occurs during mitotic cell division in the soma, and sometimes also during the meiotic divisions in the germline that give rise to sperm or eggs. Therefore, offspring sometimes inherit epigenetic variations.

Epigenetic inheritance (Jablonka & Lamb 2010)

Cellular epigenetic inheritance

Mitotic & Meiotic cell divisions
Cellular differentiation

Epigenetic Inheritance Systems (EISs):
1. Self-sustaining feedback loops.
2. Structural inheritance.
3. Chromatin marking.
4. RNA-mediated inheritance.

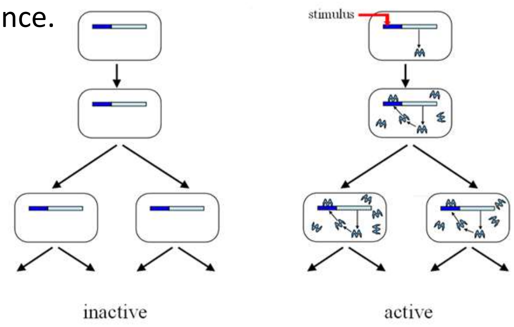
Monozygotic twin mice, *agouti* gene promoter silenced in the brown (right) mouse, as a consequence of folic acid in the mother's diet

Epigenetic inheritance (Jablonka & Lamb 2010)

Cellular epigenetic inheritance

Epigenetic inheritance systems (EISs):
1. Self-sustaining feedback loops.
2. Structural inheritance.
3. Chromatin marking.
4. RNA-mediated inheritance.

When gene products act as regulators that directly or indirectly maintain their own transcriptional activity, the transmission of these products during cell division results in the same states of gene activity being reconstructed in daughter cells.



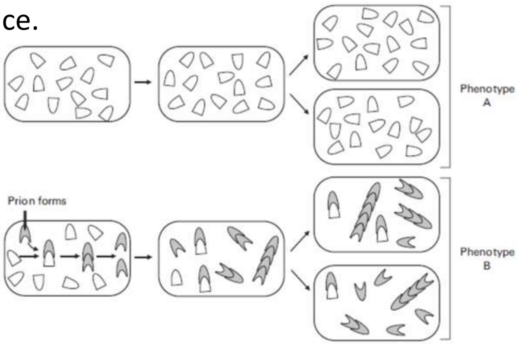
A mRNA or protein product of a gene stimulates transcription of the gene.

Epigenetic inheritance (Jablonka & Lamb 2010)

Cellular epigenetic inheritance

Epigenetic inheritance systems (EISs):
1. Self-sustaining feedback loops.
2. Structural inheritance.
3. Chromatin marking.
4. RNA-mediated inheritance.

Pre-existing cellular structures act as templates for the production of similar structures, which become components of daughter cells.



Structures are replicated using a template or scaffold structure on the parent (e.g. prions).

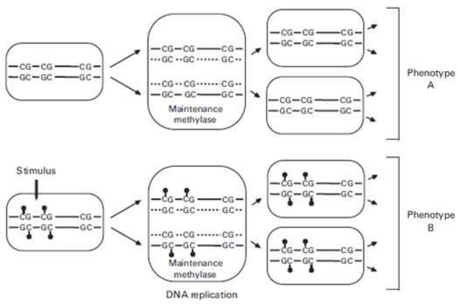
Epigenetic inheritance (Jablonka & Lamb 2010)

Cellular epigenetic inheritance

Chromatin marks: proteins and small chemical groups (such as methyls) attached to DNA, which influence gene activity. They segregate with the DNA strands during replication and nucleate the reconstruction of similar marks in daughter cells.

Epigenetic inheritance systems (EISs):
1. Self-sustaining feedback loops.
2. Structural inheritance.
3. Chromatin marking.
4. RNA-mediated inheritance.

Methyl or acetyl groups bind to DNA nucleotides or histones thereby altering gene expression patterns.



Inheritance of methylation patterns

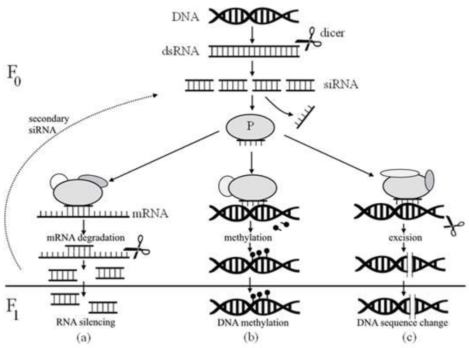
Epigenetic inheritance (Jablonka & Lamb 2010)

Cellular epigenetic inheritance

Ex.: silent transcriptional states are actively maintained through repressive interactions between small, transmissible, replicating RNA molecules and the mRNAs to which they are partially complementary.

Epigenetic inheritance systems (EISs):
1. Self-sustaining feedback loops.
2. Structural inheritance.
3. Chromatin marking.
4. RNA-mediated inheritance.

Small RNA strands (RNAi) interfere with the transcription of DNA or translation of mRNA (known only from a few studies, mostly in Caenorhabditis elegans*)*



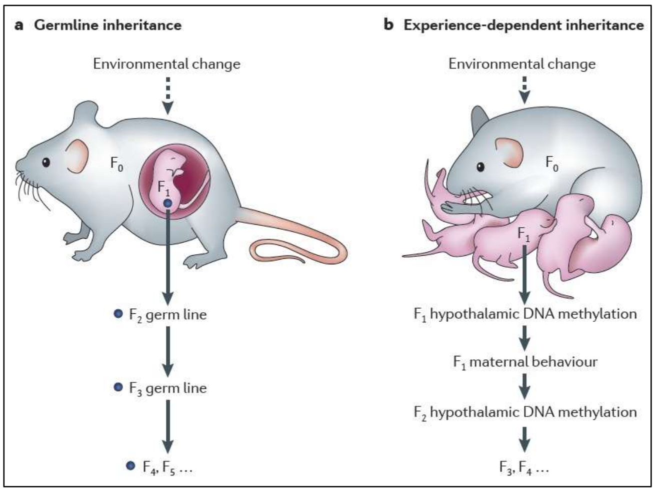
Epigenetic inheritance (Jablonka & Lamb 2010)

Developmental endowments and ecological legacies

It is not clear how much information in addition to that transmitted through DNA sequences is passed to offspring by the germline cell-to-cell route. It used to be assumed that the **size of sperm** means they can carry little information other than that in DNA, but it is now acknowledged that fathers transmit a lot through the cellular epigenetic routes we have just described. Mothers have additional routes of information transfer through materials in the egg and, in mammals, through the womb and milk. Both parents can also transfer information through faeces, saliva, and smells.

Modes of epigenetic marks' inheritance

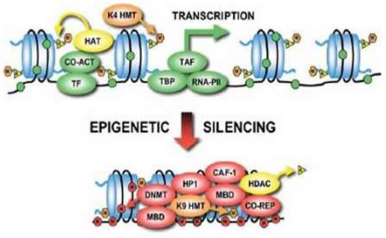
a. Germline epigenetic inheritance
b. Experience-dependent epigenetic inheritance
(epigenetic marks recreated each generation)



Danchin et al 2011

Germline epigenetic inheritance

1. genes-environment interactions during development
2. "silencing" of DNA sequences by metilation
   ("especialization" of cells in different tissues)
3. "metilation" extended to germinative cells' DNA

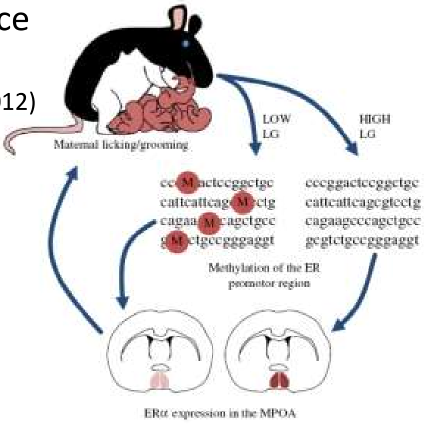


Linaria vulgaris (Cubas et al 1999)

In germline epigenetic inheritance, **an environmental effect occurring during development results in an epigenetic change within the first filial generation (F1) offspring's germ line that is transmitted to F2 offspring, F3 offspring, and so on**. Examples of this process have been observed in rodents after exposure to endocrine disruptors, as shown, and in inherited epigenetic marks that affect flower symmetry, which have been transmitted for over 250 years in some plants.

Experience-dependent epigenetic inheritance

Rats: epigenetic inheritance of style of maternal care
(Frances Champagne 2008, 2010, 2012)

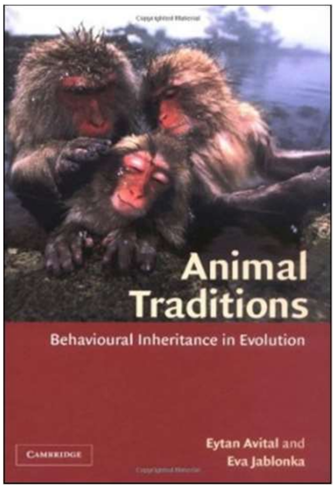


In experience-dependent epigenetic inheritance, **the epigenetic marks in the caring parent modify their behaviour in a way that provokes the occurrence of the same epigenetic marks in their offspring**. The behavioural change thus recreates the epigenetic marks de novo at each generation. An example is that of variation in maternal care in rodents).

Behavioral Inheritance: animal traditions
Avital & Jablonka 2000

Transfer of visual or auditory information through socially mediated learning (non-imitative and imitation-based).

Vocal & motor imitation.



Information transmission by the body-to-body route, whether through substances or through behavior, has very different properties from transmission by the genetic and epigenetic cell-to-cell route:

Behavioral Inheritance: animal traditions
Avital & Jablonka 2000

Information can be inherited from foster parents and, with imitative and non-imitative social learning, from related or unrelated members of the group or even from other species;

With behavioral transmission, in order for a habit, skill, preference, or other type of knowledge to be transmitted, it has to be displayed;

Unlike most new information transmitted by the cellular route, new behaviorally transmitted information is not random or blind.

Social learning that does not involve symbolic communication is as common in humans as in other mammals.

Symbol-based information transmission
Jablonka & Lamb 2005

We defined a **symbolic system** as a rule-bound system in which signs refer to objects, processes, and relations in the world, but also evoke and refer to other symbols within the same system.

Symbolic communication extends the quality, quantity, and range of the information transmitted, and, as symbols are units of meaning (words, sentences, images, vocal units, etc.), they are amenable to combinatorial organization, which can be recursive and theoretically unlimited in scope.

The symbolic system of communication enables reference not only to the here and now, but to past, future, and imaginary realities.

Symbol-based information transmission
Jablonka & Lamb 2005

Language is an excellent example of a symbolic system of communication, but so too are mathematics, music, and the visual arts. The various symbolic systems are, however, different – the type of modularity in each system, the "mobility" of the "units," and the types of principles binding the system together are not the same and apply to different levels of individual and social organization. Symbolic information, like all information transmitted behaviorally, can be passed to unrelated individuals, but unlike [behavioural] information, it can also remain latent and unused for generations (most obviously with written words).

Symbol-based information transmission also enables humans to communicate with themselves: the symbolic mode of communication is a mode of thought.

Behavior-driven evolution: genes as followers
Jablonka 2007

"Since a genetic change is only one of the types of changed input that can generate a variant inherited phenotype, there is no need to assume that a genetic change is needed to initiate an evolutionary change"

EvoDevo & Life History

Development and behavioural plasticity

juvenile capuchins' "circle play"

human object play

Evolutionary Developmental Biology: the evolution of development

Laland et al 2008

All metazoans share a **common ''tool kit'' of master regulatory genes** that govern the formation and patterning of bodies.

Regulatory genes: coordinated changes in suites of characters

Developmental processes bias and constrain evolutionary pathways.

Ecological developmental biology stresses **the roles of developmental plasticity in evolution**, especially in the formation, preservation, and prevention of novelty. The focus is the ability of the developing organism to sense cues from its environment and to modify its development to become more fit in a particular habitat.

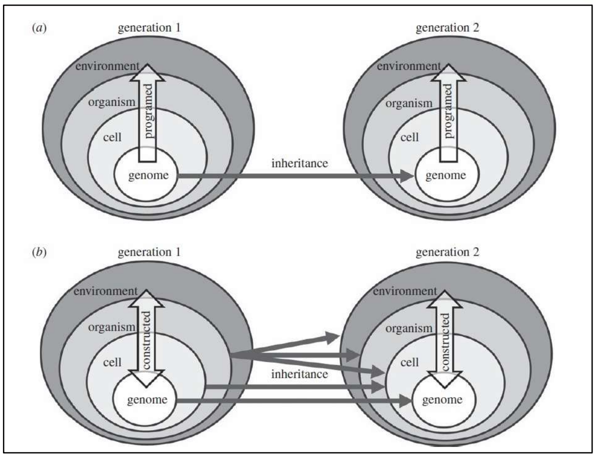
Evolutionary developmental biology: evolution of development
Laland et al 2008

Ecological developmental biology posits that **environments, as well as genes, are sources of cues for the construction of phenotypes.** Whereas classical evolutionary theory sees the organism as the key that has to fit into the environment's lock, both **ecological developmental biology** and **niche construction** see interactions between them.

Niche construction emphasizes the ability of the organism to alter its environment;
Eco-devo emphasizes the ability of the environment to alter the developing organism.

The extended evolutionary synthesis
Laland *et al* 2015

Contrasting views of development



Programmed x Constructive development
Reciprocal causation

Social learning and primate life history

Whiten & van de Waal 2018

Behavioral Ecology and Sociobiology (2018) 72:80
https://doi.org/10.1007/s00265-018-2489-3

REVIEW

CrossMark

The pervasive role of social learning in primate lifetime development

Andrew Whiten[1] · Erica van de Waal[2]

Received: 11 December 2017 / Revised: 22 March 2018 / Accepted: 29 March 2018

Abstract
In recent decades, an accelerating research effort has exploited a substantial diversity of methodologies to garner mounting evidence for social learning and culture in many species of primate. As in humans, the evidence suggests that the juvenile phases of non-human primates' lives represent a period of particular intensity in adaptive learning from others, yet the relevant research remains scattered in the literature. Accordingly, we here offer what we believe to be the first substantial collation and review of this body of work and its implications for the lifetime behavioral ecology of primates. We divide our analysis into three main phases: a first phase of learning focused on primary attachment figures, typically the mother; a second phase of selective learning from a widening array of group members, including some with expertise that the primary figures may lack; and a third phase following later dispersal, when a migrant individual encounters new ecological and social circumstances about which the existing residents possess expertise that can be learned from. Collating a diversity of discoveries about this lifetime process leads us to conclude that social learning pervades primate ontogenetic development, importantly shaping locally adaptive knowledge and skills that span multiple aspects of the behavioral repertoire.

...pported by a diversity of innova- ...further below). These have often ...ent conclusions (Whiten 2012; ...s), although there is also ample

Phase 1. Learning from mother or other primary attachment figure. Baboon infant sniffs novel food mother is eating. Photo: A. Whiten

Phase 2. Selective learning in an expanding social world. Juvenile capuchin observes expert adult male nut-cracking . Photo: T. Falótico

Phase 3. Learning from residents after migration. Male vervet switches to eat colored corn preferred by new group. Photo: E. van de Waal

Fig. 1 Three proposed major phases in the ontogeny of social learning in monkeys and apes. For full explanation, see text

Human Life History

Bogin & Smith 1996
Evolution of the Human Life Cycle

Social mammals have three basic stages of postnatal development: infant, juvenile, and adult. Some species also have a brief female postreproductive stage. The human life cycle, however, is best described by five stages:
infant, **child,** juvenile, **adolescent**, and adult.

Women in both traditional and industrial societies may also have a long post-reproductive stage. Analyses of bones and teeth of early hominids who died as subadults suggest that the evolution of the new life stages of childhood and adolescence are not of ancient origin. The current human pattern evolved after the appearance of *Homo erectus*.

It is hypothesized that the new life stages of the human life cycle represent feeding and reproductive specializations of the genus *Homo*.

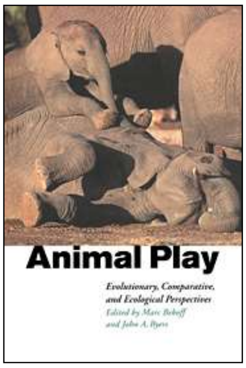
Childhood as an adaptation?

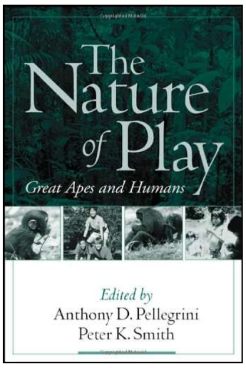
(x by-product of developmental constraints: big brains etc)

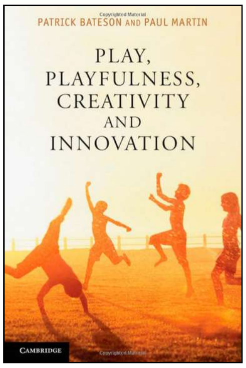
If so, to which selection pressures?
- Parental reproductive strategies
- Opportunities for social learning

Csibra and Gergely 2011:
"the **co-evolution of the uniquely long childhood period and the cooperative breeding practices in early hominins** is supplemented by the emergence of a communication system that provided 'food for thought' for the not only metabolically but also informationally hungry developing brain of children"

Play





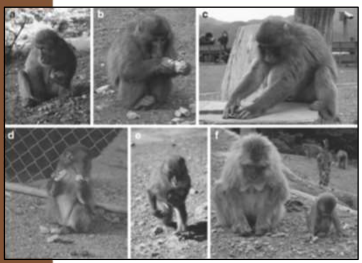


Play during the juvenile period is a low-cost strategy for developing phenotypes that will be adaptive to individuals' current and subsequent environments (Pellegrini 2008)

Mammals, birds… ?

Object play, social play, pretend play ("Make-believe").

Play



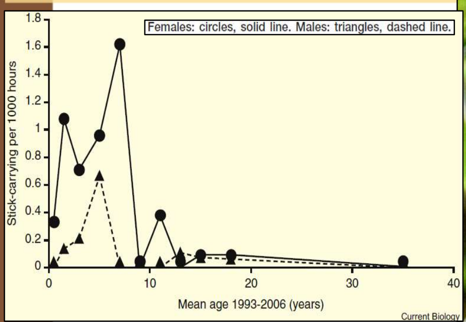
Stone handling by Japanese monkeys (*Macaca fuscata*) Huffman et al 2010

Stone manipulation

Tufted capuchin monkeys' (*Sapajus sp*) "circle play"

Play fight

Play



Young female chimp carrying stick.
Kanyawara population, Mahale Mountains National Park, Tanzania

Not yet seen in other populations – nor in adults; do young females learn from each other?

Kahlenberg & Wrangham 2010

Play

Richard Wrangham: BBC interview, 2016

Human Life History

Bogin (1997)
Evolutionary Hypotheses for Human Childhood

Heterochrony (evolutionary process that alters the timing of growth stages from ancestors to their descendants) **X childhood as a unique developmental stage of humans**.

Biological constraints of childhood: immature dentition, small digestive system, and a calorie-demanding brain that is both relatively large and growing rapidly: **the youngster is weaned from nursing but still depends on older people for feeding and protection**.

Childhood evolved as a new stage hominid life history, first appearing, perhaps, during the time of *Homo habilis*. The value of childhood is often ascribed to learning many aspects of human **culture**. It is certainly true that childhood provides "extra" time for brain development and learning. However, **the initial selective value of childhood may be more closely related to parental strategies to increase reproductive success. Childhood allows a woman to give birth to new offspring and provide care for existing dependent young.**

Evolutionary hypotheses for human childhood
Bogin (1997)

Traditional explanations for childhood:

1) Extended period for brain growth;
2) Time for the acquisition of technical skills
3) Time for socialization, play, development of complex social roles and cultural behavior.

Five additional reasons for the evolution of childhood:

1) Childhood is a feeding and reproductive **adaptation**.
2) **Releasing stimuli** for parental behaviors in the pattern of growth of the children (allometry of the growth of the human child releases nurturing and care-giving behaviors in older individuals).
3) Children are relatively inexpensive to feed (slow body growth).
4) Child care becomes even less onerous ("babysitting" is possible).
5) Childhood allows for developmental plasticity.

Evolutionary hypotheses for human childhood

Infancy and childhood as "exaptations"?

Hypotheses for the evolution of human longevity and of menopause

Large brains and longevity (Isler & van Schaik 2009): **the expensive brain hypothesis** (animals with large brains have reduced rates of growth and reproduction, but also increased total lifespan)

Menopause: human and short-finned pilot whale (*Globicephala macrorhychus)*

Is menopause an **adaptation** or a **by-product** of extended life expectation?

Hypotheses for the evolution of human longevity and of menopause

Williams GC (1957): Human post-reproductive survival: largely a product of civilization? Menopause as adaptation: an early/abrupt cessation of reproduction, due to prolonged childhood and increasingly hazardous pregnancies?
("stopping early")

X

Hawkes et al (1998), Hawkes (2003)
Chimpanzees also have extended infant care, but no post-reproductive survival; Human PR survival not restricted to industrialized societies (Ex.: Hill & Hurtado 1997 [Ache], Howell 1979 [!Kung], Blurton-Jones et al 1992 [Hadza]).

Evolution of mother-child food-sharing.

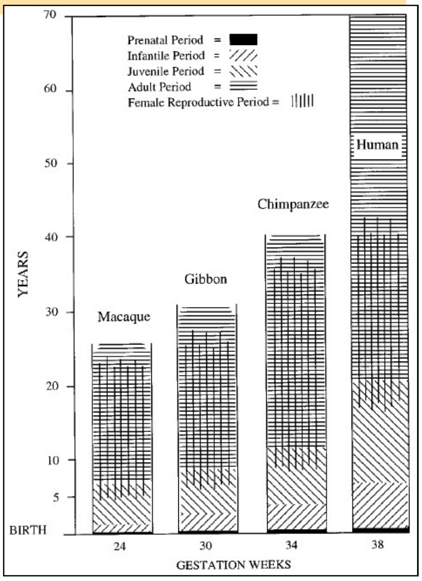
Kung-san grandmother

Hypotheses for the evolution of human longevity and of menopause

Human reproduction does not end early in comparison with other apes.

Human life history:

1) Potential longevity
2) Late maturity
3) Midlife menopause
4) Early weaning with next offspring produced before the previous infant can feed itself.



Hawkes 1998, mod. from Schultz 1969

Hypotheses for the evolution of human longevity and of menopause

Is menopause an adaptation or a by-product of extended life expectation?

Maternal investment: fitness costs of prolonged fertility + physiological trade-off favoring efficient early reproduction (Peccei 2001)

The Grandmother hypothesis
(Hawkes/ Blurton Jones)

Two-sex learning- and skills-based hypothesis
(Kaplan et al 2000)

The "Grandmother Hypothesis"

Hawkes et al (1998), Hawkes (2003), Kim et al (2012)
Hawkes & Coxworth (2013)

Two evolutionary explanations for aging: **mutation–selection balance** and **inter-temporal tradeoffs in reproductive effort**. Grandmothering could slow aging by either means.

1. Strengthening **selection against late-acting deleterious mutations** by increasing the contribution to descendant gene pools of longer-lived females through the increased reproductive success of their daughters.
2. Changing the tradeoffs between opposing effects expressed at different ages. **Increased "somatic effort"** that slowed aging at the cost of **lower "reproductive effort" at younger ages** (the contributions of senior females would increase the reproductive success of childbearers more than enough to offset the reduced expenditure of the childbearers themselves)

The "Grandmother Hypothesis"

Hawkes & Coxworth (2013)

Charnov (1993): adult mortality determines an optimal age at maturity. When mortality is high and adult life spans are short, selection favors early maturation because those who wait are more likely to die before reproducing. When mortality is low, the cost of waiting goes down; net advantage goes to delaying maturity to reach a larger adult size. Larger mothers can allocate more to offspring.

While age at first birth and average adult life spans are notably higher and longer in humans, Charnov showed that the relationship between these traits is the same for us as for other primates. Yet, unlike other primates, human adults have life spans that include a postfertile stage.

Helpful grandmothering could explain the **shorter birth intervals of humans** than the other great apes, the evolution of our exceptional **longevity** with its postfertile stage, and the evolution of our **later age at first birth**.

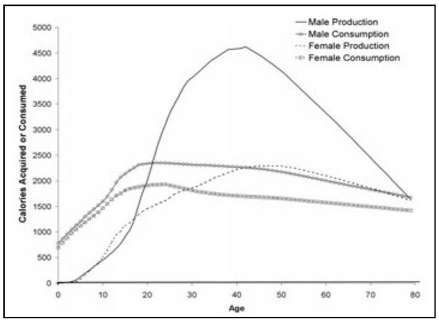
Kaplan et al (2010)
A “learning” theory of human reproductive decline and cessation

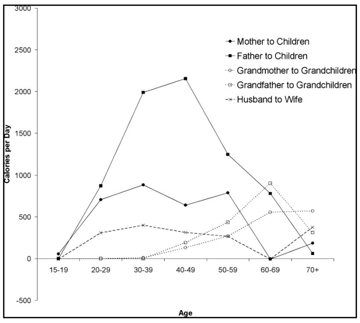
Human productivity is determined by both physical condition and long-developing skills, it is more important to survive long enough and maintain good enough condition to reap the rewards of earlier investments in skill development.

While **the returns to late-age reproduction are reduced, the returns to old-age kin investment are increased for humans** relative to other animals.

Kaplan et al (2010)
A “learning” theory of human reproductive decline and cessation

High-skill human foraging niche has a series of implications, which disfavor old age reproduction and favor old-age production and kin investment for both women and men, and thus drive the evolution of human reproductive decline and menopause.

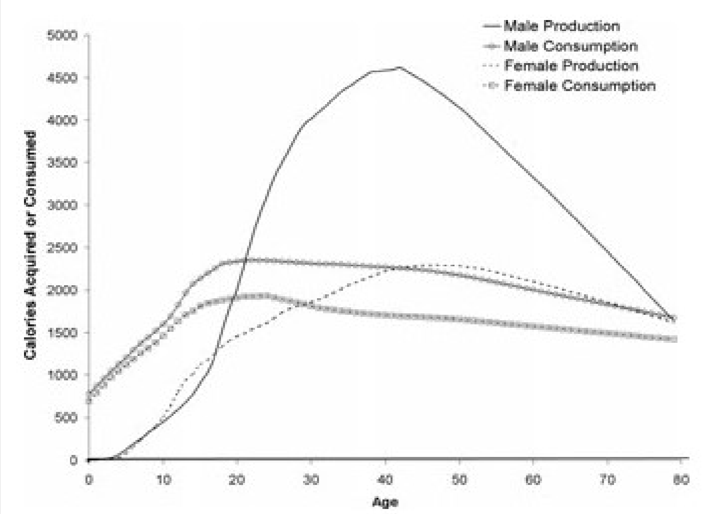




Disjunction between economic and physiological aging: human economic productivity continues to increase even after physical condition begins to decline.

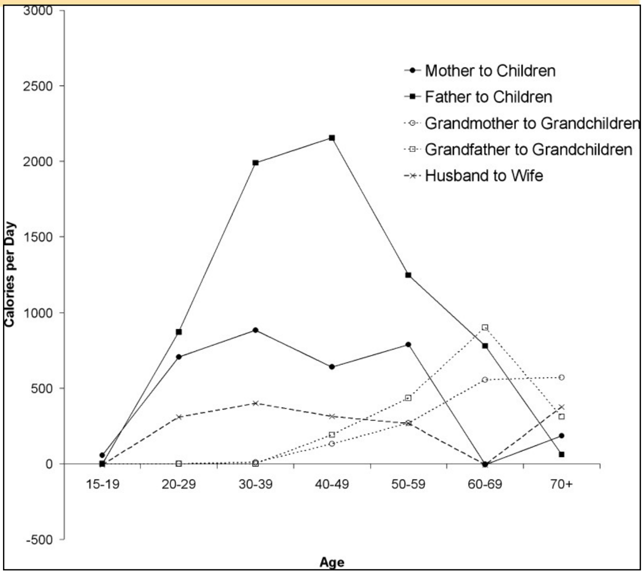
Kaplan et al (2010)
A “learning” theory of human reproductive decline and cessation

Age-specific caloric production and consumption profiles for the Tsimane (lowland Bolivia)



Peak physical condition in humans occurs in the early to mid-20s, but that peak economic productivity does not occur until after age 40, due to the fact that skill acquisition and learning continue to increase after peak physical condition is reached.

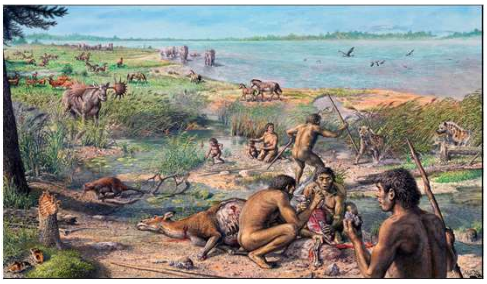
Kaplan et al (2010)
A “learning” theory of human reproductive decline and cessation



Net caloric transfers between kin groups across three generations.

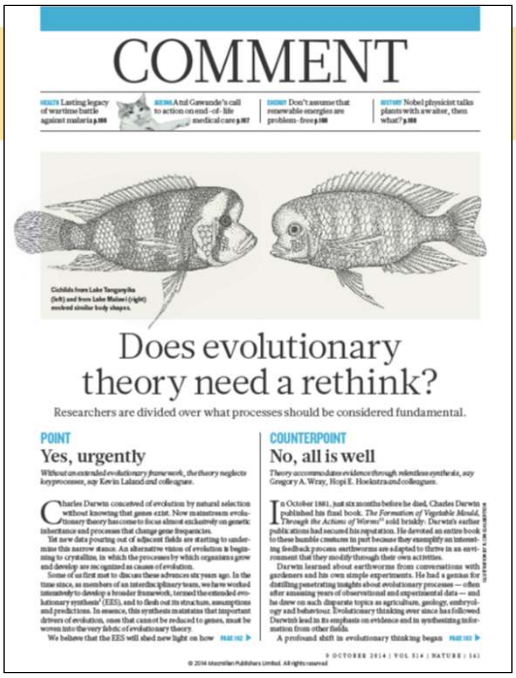
Kaplan et al (2010)
A "learning" theory of human reproductive decline and cessation

The traditional hunter-gatherer pattern of production, reproduction, and parental investment depends fundamentally on a cooperative **division of labor** between men and women (sex-specific specialization in hunting by men, and high returns to male parental investment; woman specialize in a mix of childcare and foraging for plant resources). Therefore, in addition to female menopause, **male reproductive cessation and post-reproductive investment** in descendants is a fundamental characteristic of humans living in traditional foraging and simple forager-horticultural economies.



Complex skills: grandparenting and cumulative culture?

Bushman grandmother (Namibia)



COMMENT

Lasting legacy of wartime battle against malaria p.166

Atul Gawande's call to action on end-of-life medical care p.167

Don't assume that renewable energies are problem-free p.168

Nobel physicist talks plants with a waiter, then what? p.169

Cichlids from Lake Tanganyika (left) and from Lake Malawi (right) evolved similar body shapes.

Does evolutionary theory need a rethink?

Researchers are divided over what processes should be considered fundamental.

POINT

Yes, urgently

Without an extended evolutionary framework, the theory neglects key processes, say Kevin Laland and colleagues.

Charles Darwin conceived of evolution by natural selection without knowing that genes exist. Now mainstream evolutionary theory has come to focus almost exclusively on genetic inheritance and processes that change gene frequencies.

Yet new data pouring out of adjacent fields are starting to undermine this narrow stance. An alternative vision of evolution is beginning to crystallize, in which the processes by which organisms grow and develop are recognized as causes of evolution.

Some of us first met to discuss these advances six years ago. In the time since, as members of an interdisciplinary team, we have worked intensively to develop a broader framework, termed the extended evolutionary synthesis[1] (EES), and to flesh out its structure, assumptions and predictions. In essence, this synthesis maintains that important drivers of evolution, ones that cannot be reduced to genes, must be woven into the very fabric of evolutionary theory.

We believe that the EES will shed new light on how PAGE 162 ▶

COUNTERPOINT

No, all is well

Theory accommodates evidence through relentless synthesis, say Gregory A. Wray, Hopi E. Hoekstra and colleagues.

In October 1881, just six months before he died, Charles Darwin published his final book. *The Formation of Vegetable Mould, Through the Actions of Worms*[1] sold briskly. Darwin's earlier publications had secured his reputation. He devoted an entire book to these humble creatures in part because they exemplify an interesting feedback process: earthworms are adapted to thrive in an environment that they modify through their own activities.

Darwin learned about earthworms from conversations with gardeners and his own simple experiments. He had a genius for distilling penetrating insights about evolutionary processes — often after amassing years of observational and experimental data — and he drew on such disparate topics as agriculture, geology, embryology and behaviour. Evolutionary thinking ever since has followed Darwin's lead in its emphasis on evidence and in synthesizing information from other fields.

A profound shift in evolutionary thinking began PAGE 163 ▶

9 OCTOBER 2014 | VOL 514 | NATURE | 161

Nature, Oct. 2014

Next lecture

Niche Construction and Evolution