Acquired Traits Revisited

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Abstract

Most biology texts villify Lamarck's concept of "inheritance of acquired characters" and leave the impression that all acquired characters are never transmitted to offspring. However, recent research indicates that this is not true! Some "acquired" traits are inherited. I profile some of these striking cases and their importance for evolution and for understanding a broader epigenetic context for heredity and ontogeny (the emerging field of "evo-devo"). Further, I discuss how such cases, even considered as exceptions, contribute to understanding the nature of science, both the role of general rules in biology and the occurrence of conceptual change, or paradigm shifts.

Key Words: *Epigenetics; epigenome; evo-devo; genetic assimilation; Lamarckism, paradigm shift; Weissmanism.*

In the February 2007 issue of *The American Biology Teacher*, Stern and Ben-Akiva "outline a lesson plan that is designed to challenge one commonly held naive idea, namely the inheritance of acquired traits." The present article suggests (and provides at least partial answers to) the following questions for teachers to consider if they wish to prepare lessons containing information that goes beyond the content of Stern and Ben-Akiva's curriculum.

- The lesson plan of Stern and Ben-Akiva may leave the reader with the impression that *all* acquired characters are *never* transmitted to offspring. Are there any examples of heritable acquired characters? If such examples exist, by what mechanisms can acquired traits become heritable?

- If the effectiveness of natural selection depends on the quantity of heritable phenotypic variation in a population, what mechanisms are known to generate this variation?

- If the inheritance of acquired characters is considered by most biologists to be a relatively rare exception to the general rule that acquired characters are not heritable, what can be learned by devoting class time to such "exceptions"?

- What is the meaning of "evo-devo" and why is it important for understanding modern evolutionary theory?

Can the study of acquired traits be used to help students prepare their minds for paradigm shifts and improve their understanding and appreciation of science as a way of knowing?

- National standards for biology curricula recommend that students should learn how science works to generate new knowledge. The history of science reveals that the life of many theories is ephemeral. Old theories are replaced or modified by the discovery of new facts of nature or new ways of interpreting existing facts (National Research Council, 1996: p. 201). This heuristic process is sometimes referred to as a "paradigm shift." Can the study of acquired traits be used to help students prepare their minds for paradigm shifts and improve their understanding and appreciation of science as a way of knowing?

Epigenetics

An acquired trait develops during the life of an organism as a consequence of a genotype that allows certain unusual environmental factors to modify developmental processes, thus producing a different phenotype than would develop in the normal range of environments (the "norm of reaction"). *Epigenetics* is a branch of genetics that studies how phenotypic variants arise without changing the nucleotide sequence in DNA.

Differential gene action is responsible for cellular differentiation; that is, different groups of genes are "turned on" or "activated" (transcribed into RNA; messenger RNA is translated into proteins) while other groups of genes are "turned off" (inactivated or silenced) in different cell types. Finding the signals that regulate when and where gene products are made and in what quantity is the key to understanding genetics, epigenetics, cellular differentiation, ontogeny, and their interrelationships in modern evolution theory (evo-devo).

We now know that many segments of noncoding DNA (not coding for proteins) contain "RNA-only" genes that can be transcribed into noncoding RNA (ncRNA) molecules but are not translated into proteins. Some of these noncoding RNA molecules (called "short interfering RNA" or siRNA) can suppress translation or promote degradation of specific mRNA molecules (Geddes, 2007; Taubes, 2009).

As a rule, the addition of methyl groups (CH_3) to DNA nucleotides (by enzymes known as DNA methyltransferases, especially in or near promoter regions of genes where transcription begins), tends to interfere

with gene transcription, whereas addition of acetyl groups ($COCH_3$) to histone proteins in chromatin tends to enhance gene transcription. These methyl and acetyl groups are known as "epigenetic tags or marks." These tags do not change (mutate) the nucleotide sequences in DNA. The pattern of epigenetic markings on chromosomes (the *epigenome*) may vary from one cell type to another and from one time to another during the life of an individual cell. Adding methyl groups to one gene may be beneficial or adaptive (e.g., silencing of a cancer-promoting proto-oncogene), but may be harmful to another gene (e.g., inactivating a tumor-suppressor gene). Histone proteins are found in association with multiple DNA regions throughout the chromosomes, whereas other nonhistone proteins (called "transcription factors") are characterized by DNA-binding segments that enable them to attach to target nucleotide sequences and regulate the transcription of specific genes.

○ Inheritance of Acquired Characters

Although it is not well understood, during the first few days after conception, most of the epigenetic tags on chromosomes of human parents are removed from the chromosomes of the embryo. By mid-gestation, new epigenetic patterns are usually established. Although most of these epigenetic patterns are not heritable (i.e., not transmitted by sexual reproduction to offspring), a few of them are. Occasionally, the methylation pattern of a parental chromosome can persist through meiosis and is found in the chromosomes of the next generation, sometimes for several generations. The following are some examples. Water fleas (genus *Daphnia*) grow defensive spines when exposed to predators. The effect can last for several generations. An epigenetic change in nematode worms has been inherited for 80 generations (Watters, 2006). When pregnant rats are exposed to the fungicide vinclozolin and the pesticide methoxychlor, their male offspring produce abnormal sperm (slow swimming, early death). These acquired characters reappear in most of their sons, grandsons, and greatgrandsons (Ruvinsky, 2006). If pregnant guinea pigs are exposed to the glucocorticoid drug betamethasone (used to hasten lung development of premature human babies), their offspring have physiological and behavioral abnormalities. These abnormalities also appeared in the grandprogeny of the females that were exposed to the drug (Motluk, 2005).

Epigenetic marks on DNA or chromatin can sometimes be changed in response to various environmental factors or patterns of behavior, and some of these marks can be transmitted from parents to their offspring, resulting in the "inheritance of acquired characters." For example, the food that animals eat may sometimes influence the phenotypes of their offspring. Yellow-haired mice tend to be fat and susceptible to life-shortening disease. When fed a diet rich in methyl donors (such as folic acid, vitamin B_{12}, onions, garlic, or beets), female yellow mice produced slender, brown-agouti progeny that lived a normal span of life. It is thought that the methyl groups in the mother's food found their way into the embryo's chromosome, became attached to the yellow gene, and silenced it (Watters, 2006).

Even some maternal behaviors can induce epigenetic changes in progeny. Newborn rat pups that are licked and groomed by their mothers mature to be relatively calm and brave. Newborns that receive little or no maternal licking grow up to be nervous and seek darkness. The hippocampus of the brain of a well-licked rat is better developed and releases less of the stress hormone cortisol than the hippocampi of rats that were deprived of neonatal licking. The methylation patterns in hippocampus cells are different in licked and nonlicked rats. These epigenetic signals can be reversed in the brains of adult rats by injection of the drug trichostatin A (Watters, 2006).

For most protein-coding genes, both maternal and paternal alleles of a gene are normally activated or inactivated at the same time. Sometimes, however, the allele of one parent is active (or inactive) while the allele of the other parent is inactive (or active). This epigenetic phenomenon is termed *parental imprinting* (Jirtle & Weidman, 2007). For example, the *R* gene in maize controls the color of pigment grains in the aleurone (outer layer of endosperm) of the kernel. If the seed parent is *RR* and the pollen parent is *rr*, the hybrid seeds are solid red. But hybrids of the reciprocal cross are mottled because the maternal copy is only partly expressed, owing to an epigenetic effect. People who receive the dominant gene for Huntington's disease show symptoms during adolescence if it is inherited from the father, but develop symptoms during middle age when the gene comes from the mother.

Human fathers who started smoking tobacco before age 11 produce sons who are heavier than sons of fathers who began smoking later in life or who never smoked; daughters are unaffected (Pennisi, 2005). Grandsons of men who consumed a surplus of food during childhood have a higher risk of developing diabetes than those whose grandfathers were reared in times of food scarcity. The health of granddaughters is correlated only with that of their paternal grandmothers (Pennisi, 2005). One of the best plant examples of a fairly stable methylation pattern transmitted over many generations is found in the peloric (Greek for "monster") flower form of the toadflax *Linaria vulgaris*. Carl von Linnaeus (1707–1778) thought that it was a new species. Today, it can still be found in the same region where Linnaeus found it (Jablonka & Lamb, 2005). Jablonka and Raz (2009) list about a hundred examples of transgenerational epigenetic inheritance.

Landman (1991) presented several examples that are defined operationally by him as "inheritance of acquired characters" (IAC) systems because they conform to the following experimental pattern:

> Individual organisms or cultures of cells incubating in a particular environment are exposed briefly to a chemical or physical treatment under conditions that allow little or no growth (thereby ruling out selection of mutants). *Following the exposure, and upon being returned to the original environment, all or a large proportion of the treated cells (or organisms) exhibit new characteristics that are passed on heritably to succeeding generations.*

Landman claimed that at least three mechanisms are known to give rise to IAC. In organisms with nucleated cells, IAC would not involve changing chromosomal genes (mutations) but might involve (1) heritable stabilization of gene expression without any attendant change in nucleic acid sequence (extranucleic inheritance; examples include the inheritance of a wall-less state in *Bacillus subtilis*, maintenance of the induced state in the *lac* operon of *Escherichia coli*, and cortical inheritance in ciliates); (2) alterations in DNA substituents, such as addition or removal of methyl or glucosyl groups (epinucleic inheritance); and (3) nucleic inheritance by horizontal or lateral gene transfer that occurs when foreign nucleic acid-containing elements such as plasmids (small circles of nonessential DNA in bacteria) or viruses are added to an organism's genome or to its cytoplasm.

○ Genetic Assimilation

There are at least two mechanisms by which acquired characters can be made heritable. As previously discussed, epigenetic methyl tags on some regions of DNA can be passed from one generation to another. *Genetic assimilation*, on the other hand, is the process by which a phenotypic character initially produced only in response to an unusual environmental influence (an acquired trait) becomes, through a process of selection, taken over by the genotype, so that it is formed even in the absence of the environmental influence that at first had been necessary (King, 1968). Studies of fruit flies in a wild population have shown that most of their traits have relatively little phenotypic variation, even though the population contains a remarkable amount of unexpressed genetic variation. Development of these wild-type characters is said to be well "canalized" or "buffered" against minor perturbations caused by genetic or environmental differences. Abnormal (mutant) flies called "crossveinless" have all or a portion of the tiny crossveins in

their wings missing. Exposing normal (wild-type) flies to an unnaturally high temperature for a few hours during their pupa stage caused ~40% of them to develop a crossveinless phenocopy. If only heat-shocked crossveinless flies were allowed to breed, the frequency of the crossveinless trait was shown to increase to over 90% in fewer than 20 generations. However, as early as generation 14, some of the flies developed the crossveinless trait even in the absence of heat-shock. Breeding only from these unshocked crossveinless flies in a normal environment produced strains in which the crossveinless trait was almost 100% (Waddington, 1953). Thus, the crossveinless trait, which was originally an acquired character, had undergone almost complete "genetic assimilation" by selection to become an inherited character that developed in normal environments (without heat shocks). This experiment shows that exposing an organism to an unusual environmental factor can reveal the cryptic genetic variation of a trait on which selection can act to produce recombinants that develop an acquired trait even without the environmental stimulus that was initially required for its production. Genetic accommodation

> differs from genetic assimilation in that the latter results in canalization of the new phenotype so that it is no longer affected by environmental variation, whereas genetic accommodation can result in an increased environmental sensitivity of a plastic phenotype. (Suzuki & Nijhout, 2006)

Palmer (2004) cited five examples of genetic assimilation and concluded that the process may be much more widespread than is currently believed.

The evolutionary potential of a population depends on the amount of heritable biological variation from which natural selection can propagate new adaptive gene combinations. The meiotic processes of genetic crossing-over between linked genes and independent assortment of homologous chromosomes into gametes are the main engines that create most new genetic combinations in a population. New gene mutations (altered DNA nucleotide sequences) are the ultimate source of most heritable biological variations. Not all acquired characters are necessarily adaptive, but like random (nondirectional, nonteleological) genetic mutants, only heritable adaptive traits are likely to persist over many generations in a population of organisms through natural selection. The effects of epigenetic modifications to DNA or chromatin, though not often transmissible from one generation to another, are occasionally inherited over several generations and may be an underappreciated source of biological variation. Pigliucci (2006) is among the visionaries who believe that

> Inherited epigenetic variants can interact with their genetic counterparts to multiply by orders of magnitude the phenotypic variation available to natural selection, thereby expanding the mechanistic basis of evolutionary theoretical explanations and greatly increasing their plausibility as an account of life's diversity.

○ Understanding the Nature of Science

French naturalist Jean Baptiste Lamarck (1744–1829) revolutionized the study of lower invertebrates, but he is best known today for popularizing the ancient theory (Plato discussed it) of the inheritance of acquired characters in his 1809 book *Zoological Philosophy*. British naturalist Charles Darwin (1809–1882) did not know the biological basis of heritable phenotypic diversity in natural populations or how new hereditary characters arose, and so he relied on IAC to fill that gap in the first edition (1859) of his book

On the Origin of Species. Without an understanding of genetics, his theory of evolution was incomplete. That is one reason why we no longer equate Darwinism with modern evolutionary theory. Creationists (now calling themselves "intelligent design advocates") continue to refer derogatorily to modern evolutionary theory as "Darwinism." In 1865, the Moravian monk Gregor Mendel (1822–1884) reported his breeding experiments with peas. He rejected the prevailing theory (paradigm) that the hereditary substance behaved as a fluid and blended in hybrids. In its place, he proposed that traits were produced by nonblending particles of heredity (later to be called "genes" by others). His work, however, did not explain the inheritance of quantitative characters that commonly are partly influenced by environmental factors. Even at an elementary educational level, it might be mentioned that all monogenic traits are not Mendelian. For example, sex-linked traits are inherited in a non-Mendelian fashion, as are traits governed by genes in mitochondria and chloroplasts. Parental imprinting is yet another non-Mendelian phenomenon. Unfortunately, teaching only Mendelism might lead some astray into "genetic determinism" ("genes are everything"), with its undesirable political and social implications (Allchin, 2005). By cutting off the tails of mice for several generations and breeding only from them, the German biologist August Weissman (1833–1914) reported in his 1891 book that the tail lengths of all the descendants grew to normal length. Many people assumed from these experiments that if characteristics acquired during the lifetime of individuals by such extreme measures had no heritable consequences, then the more subtle effects of natural environmental factors would also be ineffective in changing their hereditary factors. Lamarckism thus fell into general disrespect as far as plants and animals are concerned. Weissmanism, until recently, became a "sacred cow," immune to challenge or change.

However, just because the ideas of these pioneering scientists were wrong or incomplete in certain respects does not justify villainizing them or bashing their ideas as worthless. Teachers should emphasize that putting forth an original idea, even a flawed one, may heuristically serve to stimulate scientific investigation to verify, falsify, modify, extend, or replace it. This is how scientific knowledge advances and accumulates.

> High school students may have difficulties understanding the views of historical figures. For example, students may think of historical figures as inferior because they did not understand what we do today. This "Whiggish perspective" seems to hold for some students with regard to scientists whose theories have been displaced. (National Research Council, 1996: p. 200)

At a more advanced level of education, students should be informed of the "tentativeness" of scientific hypotheses or theories. A prevailing concept today (paradigm) may be discarded tomorrow by the discovery of new facts of nature. The general public tends to view a scientific paradigm as a sacred cow. The current debate over when women should receive mammograms has left many women dismayed and emotionally conflicted. They thought that science had proved the value of early mammograms in detecting breast cancer, and now they are being told that it may not be the best procedure. The public's view of scientific authority is shattered by these kinds of challenges to an accepted paradigm. The discovery of the enzyme RNA-dependent DNA polymerase proved to be an exception to the "central dogma" of molecular biology (DNA → RNA → protein) that some may consider a minor deviation from the general rule. However, this enzyme became a hallmark of a taxonomic class of viruses known as retroviruses. Human immunodeficiency virus (HIV) is a retrovirus that causes acquired immunodeficiency syndrome (AIDS), which is now epidemic throughout the world. Similarly, the recent discoveries of the "epigenome," regulatory RNA molecules, and epigenetic tags

added to target DNA sequences by methyltransferase enzymes cannot be considered trivial because turning genes on or off during embryological and postnatal development is at the heart of how organisms develop their anatomical, physiological, biochemical, and behavioral traits.

○ On-Line Teaching Supplements

A Survey to Evaluate Students' Understanding of Reproduction, Heredity, Ontogeny, and Phenotypic Diversity; Lists A and B (http://www.jstor.org/stable/10.1525/abt.2011.73.2.6)

NOVA program "Ghost in Your Genes" (http://www.jstor.org/stable/10.1525/abt.2011.73.2.6)

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