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The Inheritance of Acquired Characters: Impossible or Inevitable?

Introduction

The idea that characters acquired during the lifetime of the individual can be inherited and play an important role in evolution has been the subject of controversy for over a century. Enthusiasm for the idea, which is usually associated with the name of Lamarck, has sometimes led to charlatanism and fraud, while opposition to it has led to "Lamarckism" being used as a term of abuse. Nowadays biologists regard the ideas about inheritance of acquired characters as no more than an interesting part of the history of biology. The inheritance of acquired characters is rejected because it is assumed there is no evidence for it, no mechanism that can produce it, and no need for it in evolutionary theory. Yet all of these assumptions can be challenged. To understand the basis for the current point of view, as well as for the challenge, it is necessary to give a brief historical overview. Where did the idea that acquired characters are inherited come from? Why did it become prevalent? Why have opinions changed? Following this historical overview, I shall present evidence showing that some acquired variations are inherited, go on to argue that the evolution of mechanisms enabling such inheritance is part of the evolution of complexity, and advocate an integrative approach, where the effects of different inheritance systems are combined.[1]

Historical background

For more than 2000 years people believed that characters acquired during the lifetime of the individual as a result of their own activities or of the effects of the environment can be inherited. This idea was based on a very broad concept of inheritance that included biological and social aspects. Status, which is often acquired, is also often inherited; acquired

[1] The ideas presented in this paper were developed by Marion Lamb and myself. Many of them are summarized in our book: *Epigenetic Inheritance and Evolution: The Lamarckian Dimension*. 1995. OUP, Oxford. The ideas in this article have been presented in a seminar in the Wissenschaftskolleg on March 17, 1998.

professions can be inherited. Among the Jews priesthood was inherited in the Levi tribe (in the Cohen lineage), and according to Homer the talent for prophecy ran in families.

The school of medicine founded in Greece by Hippocrates in the 5^{th} century B.C. developed a detailed, materialistic theory of inheritance. The focus of the theory was a hereditary substance called "semen", its formation and its effects. The Hippocratic doctors suggested that each part of the body forms special semen. It is formed both in the male parent and in the female parent and is transported to the reproductive organs. During the sexual act the male and female contributions are mixed. The fact that all the parts of the body produce semen explains why children tend to be similar to their parents: if the blue eyes of the parents reappear in the offspring, it is because the eyes of the parents produce a special blue-eye contribution to the semen. The blue-eye semen of the male and female parents combine in the offspring and determine its eye colour. If some parts of the body are diseased or weakened, the semen coming from this part will also be diseased and weakened, and the offspring will inherit the infirmity of the parent. Acquired characters are inherited, according to this theory. Sex, too, was thought to be determined by the potency of the male and female semen. The male semen was considered strong and the female's semen weak; their relative quantities and potencies determined the sex of the offspring.

Various versions of the Hippocratic theory were perpetuated throughout the centuries. During the 18th and 19th century, when the biological sciences were flourishing, variants of the Hippocratic theory abounded. Darwin, for example, developed a detailed heredity theory which was very similar to the Hippocratic theory. He postulated the existence of tiny hereditary particles called gemmules that represented the various traits of the organism. These particles were released from the cells of the body and accumulated in the reproductive organs, forming the hereditary material of the parent. Changes in organs and traits that occurred during the development of the parents affected the gemmules and hence were inherited by the progeny. Darwin called his heredity theory "the theory of pangenesis", and this is the general name currently used for this class of heredity theories.

During the 19th century, the development of agriculture led to more systematic animal and plant breeding, and this increased the interest in theories of inheritance. People began asking explicit questions such as what is inherited and how. No less important was the construction and the growing importance of evolutionary theories. The idea that present-day living organisms evolved from earlier and often simpler forms focused attention on heredity, because evolutionary theories all assume that hereditary variations must be transmitted to descendents and have cumulative effects. The origin and the generation of hereditary variations became an important issue.

Lamarck, the first great evolutionist, used the idea that acquired characters are inherited as one of the two major driving forces in his theory of organic evolution. The first driving force was the self-complicating trend, inherent, according to Lamarck, in biological organization; the second was adaptation to changing environments through the inheritance of acquired characters. Darwin, too, believed in the inheritance of acquired characters, as his pangenesis theory clearly shows. However, he thought that the major force of evolution was the selection of heritable variations, rather than the generation of adaptive variations. Darwin believed that many variations are random, in the sense that they are not an adaptive response to the environmental changes that the organism experiences, although he believed that some are induced by the environment. Variation, the inheritance of variations, and multiplication are the necessary conditions for Darwinian evolution. Natural selection is a logical emergent necessity in a system with these properties, when resources are limited. The origin and generation of variation is not specified by Darwin's selection theory.

From the middle of the 19th century onwards, the relative importance of the selection of variations and the generation of acquired variations in evolution was hotly debated. Most people believed that acquired variation can be inherited, but there was beginning to be strong opposition to the idea. The most effective opponent was the great German evolutionist, August Weismann. In time, his arguments were widely accepted, and as they were combined with new discoveries about the cell, about the rules of inheritance, and about the hereditary material, the idea that acquired characters can be inherited was questioned and finally rejected. Since I am going to challenge the still widely-accepted view that acquired characters are not inherited, I want to look more closely at the arguments and discoveries that led to it.

August Weismann opposed the idea that acquired characters were inherited for three main reasons. First, he re-analyzed the data that was supposed to support this claim and found it deficient or based on fictitious evidence. There was simply no empirical support for the assertion that acquired characters are inherited. He also showed that it ignored well-known facts. For example, despite the Jews' practice of circumcision for the last 3000 years, the ritual has to be repeated every generation: the lack of foreskin does not become inherited.

Second, Weismann argued that the mechanisms of individual development from a fertilized egg to an adult organism do not allow the inheritance of acquired characters. He thought that, as the fertilized egg undergoes cell division and becomes a multi-cellular organism, the different cells must alter their hereditary characteristics to become typical specialized body cells (somatic cells) – liver cells, kidney cells, brain cells, skin cells, and so on. Specialization, he believed, depends on changes in the hereditary material within the cells. The only cells that maintain their original hereditary composition are those that develop into sexual cells (the germ-line). They are the link between generations. Therefore, Weismann argued, only changes in these germline cells can have effects on the next generation. The somatic cells are an evolutionary dead-end – whatever happens in them cannot have any effects on the next generation, because these cells can never become the fully potent germ-line cells with all the material necessary for the next round of development. Because only germ cells provide the link between generations, and because he assumed that somatic cells could not be transformed into germ cells, Weismann deemed the inheritance of somatically acquired characters impossible.

The third and most important reason for Weismann's rejection of the idea that acquired characters can be inherited was also based on developmental considerations. If a somatic character (for example, the size of the muscles) changes as a result of changes in the environment (such as a lot of exercise), how can this change be communicated to the germ-line, to the sex cells? How is the information about the size of the muscles to be carried from muscles to sex cells? He saw no conceivable way to achieve this translation from the chemical "language", in which the character is expressed in the muscle tissue, to the very different chemical "language" of the sex cells. He therefore rejected the idea that such information can be transmitted. With the notable exception of Aristotle, Weismann was one of the first biologists to think about organisms in terms of information.

At the turn of the century, this belief that acquired characters are not passed on, was reinforced by the discovery of Mendel's laws of inheritance. The transmission of Mendelian traits (especially those that were chosen for analysis) is generally reliable. It is not changed by changes in environmental conditions. Mendel suggested that sexually reproducing organisms have two sets of hereditary information, one contributed by the mother and one by the father. The hereditary factors of a particular pair can be identical (the organism is then said to be "homozygous" for these factors) or they can be somewhat different (the organism is then said to be "heterozygous" with respect to such a pair). Each offspring is formed from the union of two parental sex cells, the sperm and egg. The formation of the sex cells involves the separation of the two sets of information, so that a sex cell contains only a single set of factors.

The behaviour of the hereditary factors was deduced by Mendel from experiments in which he carried out controlled matings (i.e. matings between parents with heritable differences in a particular trait). Mendel showed how we can infer that a trait-difference is due to a difference between hereditary factors. For example, we can infer how the hereditary factors determining seed colour in peas behave, from the ratios of different coloured peas (the ratio of green versus yellow peas) we get form controlled matings. But for that inference to be reliable, the development of seed colour should not be too sensitive to environmental fluctuations and the factors must have clear effects.

As genetics continued its development in the early years of the 20^{th} century, it became evident that the relationship between the hereditary factors and the traits of the organism is very complex. The old terms of the 19th century were no longer adequate to describe this relationship. Soon the Danish geneticist Wilhelm Johannsen invented three major terms that have become the basis for the thinking about heredity ever since: genotype, phenotype, and gene. “Genotype” refers to the genetic constitution of an individual, and the gene is the unit of the genotype, the old “hereditary factor”. The term genotype is used for both the inherited potential to develop a particular character, such as green eyes or tall stature, and also, more generally, for the sum total of all the genes in the individual – the total developmental potential, or information. The “phenotype” is the realization and manifestation of the potential, the actual product. Exactly how the potential is realized depends on the environment. One of the important corollaries of the phenotype/genotype distinction is that the visible trait, the phenotype, may not be rigidly specified by the genotype. What an organism becomes depends on the genotype and on the environment in which this genotypic potential is realized. If the environment varies, the phenotype can vary too. However, as Johannsen stressed, it is the genotype alone, the hereditary potential, that is inherited. The phenotype, the realization of this potential, is not inherited.

The discoveries of molecular biology in the second half of the 20^{th} century revealed how genetic information is stored and processed. These discoveries reinforced the belief that characters acquired during development cannot be inherited. It was discovered that DNA is the genetic material, the genotype, the hereditary potential. DNA is essentially a linear molecule built of four types of repeating units called nucleotides. It is useful to compare DNA sequences to written language. If we think about the linear array of the units as a written message, and about the four nucleotides as four different letters, we immediately see that many messages are possible. As in written language, different DNA stretches will be different not because the components differ, but because their sequences differ. Only the length of the molecule limits the number of possible ways in which these four units can be linearly organized. The gene is seen as a DNA sequence, directly coding for or regulating the manufacturing of a protein, a building block of the body. The relationship between the DNA (the potential, the genetic information) and the protein (the phenotype, the actual realization of the information) was established with these discoveries. The central dogma of molecular biology asserted that the flow of information in biological systems is unidirectional: from DNA to protein, but not vice versa. Thus, changes occurring in proteins cannot affect the DNA. It is the DNA alone and variations in DNA alone which are inherited. Proteins and variations in proteins are not inherited. The notion that acquired characters can be inherited seemed at last dead and buried by the molecular discoveries.

I have done my best to present the line of reasoning and discoveries leading to the conclusion that acquired characters cannot be inherited. Let me now challenge this conclusion by looking again at the major assumptions underlying it: a. Heredity and genetics are the same thing. Only genes, and variations in genes, are inherited. b. Heritable variations are accidental, not acquired, because there is no way in which adaptively acquired information can be transferred from proteins back to genes. (This assumption is, of course, a corollary of the first one).

In the following sections I shall argue that the current concept of heredity, which identifies it with genetics, is too narrow, and does not incorporate current knowledge. Not only DNA is inherited, and not only variations in DNA are inherited. There are at least three additional inheritance systems that can lead to the transmission of heritable variations, some of which are acquired during the lifetime of the organism. I shall suggest that evolution often leads to the development of mechanisms allowing the inheritance of acquired characters. The mechanisms for the inheritance of acquired characters are important adaptations that have evolved several times at different levels of biological organization. Finally, I shall try to demonstrate that, to account for traits and behaviours and gain a better understanding of evolution, we have to consider and integrate all the systems of inheritance.

Evidence and mechanisms for the inheritance of acquired characters: The systems of inheritance

Before briefly describing the different systems of inheritance and the way in which information is acquired, stored, and transmitted through them, I would like to comment on Weismann's objections to the inheritance of acquired characters. First, unlike the situation in Weismann's time, good empirical evidence for the inheritance of some acquired variation is now available. Second, the segregation between body cells (soma) and the lineage producing the sex cells (germ line) is not as general or as rigid as Weismann thought. In many groups of living organisms, including all plants and many animals, body cells can be transformed into sex cells. In these groups, variations acquired by the somatic cells can become variations of germ cells and can be transmitted to subsequent generations. Finally, the problem of the transfer of information from soma to germ line may not be so acute if somatic cells become sex cells, so that somatic information becomes germ line information. Even information from higher levels of organization (systems, tissues) can be inherited, if, as I argue, not only genotypes but phenotypes, too, are transmitted between generations.

DNA inheritance – more than just random mutations?

The most fundamental inheritance system in living organisms is the DNA inheritance system. We have recently learnt, that this system is a lot more sophisticated that we once thought. Until ten years ago, the origin of variations in DNA was thought to be due only to chemical damage, errors during the process of DNA replication, errors that were created during DNA repair, or changes due to the movements of genomic parasites. Although many variations in DNA do have such an accidental origin, it seems now that, in microorganisms (such as bacteria), some variations are the result of changes in DNA introduced by enzymes whose role is to manipulate DNA. Each cell contains a genetic "engineering kit" which can be mobilized under the right conditions and may lead to the introduction of variations that are more likely to be adaptive than if the process was completely accidental. The literature on this issue is quite technical and the interpretation of data is controversial, so I shall not go into it here. I only want to point out that even the DNA inheritance system is far from being fully understood. What is clear is that DNA is not merely a passive information carrier; it can also function as a response system.

Cellular heredity

The second system of inheritance is the cellular heredity system. Even when cells have exactly the same DNA sequence, cells with different phenotypes may transmit their special characters through cell division. Since at the DNA level the cells are all identical, the variation and the processes underlying its transmission is additional to and different from the DNA system. We are, in fact, well acquainted with this type of systems – there at least 200 cell types in our body (skin cells, liver cells, kidney cells, and so on) that all have the same DNA but differ from each other in shape, content, and function. These cellular variations are transmitted through cell division when the cells multiply – the different cells can be said to breed true. We are beginning to understand this type of cellular (or epigenetic) heredity, and can recognize three types of cellular heredity systems. I will not go into a great deal of detail describing them, because they are quite complex biochemical systems. I shall only illustrate with very simple (and somewhat simplified) schemes what they are and point to the evidence showing that such cellular variations can be transmitted between generations.

The first epigenetic inheritance system is based on the perpetuation of functional states through positive feedback loops. In the simplest case, a gene is activated by an external signal, and as a result of this activation produces a new protein product and a changed phenotype. The new product has a regulatory function – it stimulates further production of itself by the gene. The external signal is now redundant, and the cell will go on producing the new product and the new cellular phenotype, even if the external signal disappears. If the new product is present in sufficient amount within the cell, when the cell divides, the two daughter cells will have enough of the product and the functional state will be perpetuated. There are many well-characterized systems of these type in all living cells, and they seem very important in the process of development.

The second type of cellular heredity system leads to the transmission of alternative cellular structures. Cell structures can sometimes template the formation of new similar structures in daughter cells. Consider two alternative structures, A and B, that are formed from the same building blocks. If type A structure is a “nucleus” for the formation of more type A structures, and type-B structure perpetuates the formation of more B structures, cells with A structures will transmit their A character through cell divisions, as will cells with B structures. Such transmission of alternative cellular structures seems to underlie the transmission of some diseases, the notorious mad cow disease, for example. In this case it seems that abnormal protein complexes (called prions) acquired through eating the meat of sick animals perpetuate the formation of more abnormal complexes. The protein building blocks in humans and the genes coding for them have not been changed, but the abnormal prions acquired from cattle now organize the human building blocks in a new, self-perpetuating manner leading to a serious and finally fatal disease. The transmission of the abnormal prions is dependent not on the DNA inheritance system, but on the special properties of the protein complexes that perpetuate the formation of more of the same: normal complexes "breed" more normal complexes, abnormal complexes "breed" more abnormal complexes. Such inheritance of architecture occurs not only with diseases, but is also part of normal development.

The third epigenetic inheritance system allows the inheritance of chromosomal states. The chromosome is not made only of DNA. Proteins, RNA and various chemical groups (which have been called chromatin marks) are attached to DNA. These chromatin marks affect and sometimes precisely control the information flow from DNA to proteins: they influence how and when genes are expressed. The same DNA sequence can have and does have a different pattern of marks in different cells. When DNA is replicated, the chromatin marks too are re-produced. There are several mechanisms for the re-generation of specific marks and specific marking patterns, depending on the chemical nature of the marks.

With all the cellular heredity systems, the cellular state can be transmitted from cell to cell. But what about transmission form one individual to its progeny? This is un-problematical in unicellular organisms, or in organisms that multiply by fragmentation, because in these cases the transmission to the next generation is more or less automatic. In sexually reproducing multi-cellular organisms like ourselves, flies, or plants, if epigenetic variations first happen in somatic cells, to be inherited by the next generation they have to be transferred to the germ-line, to the sex cells. This is more tricky, and it depends on whether or not somatic cells can become sex cells. As I mentioned before when discussing Weismann's objections to the inheritance of acquired characters, in plants and many animals groups, somatic cells can become sex cells. There is therefore no reason why epigenetic variations should not be transmitted. In plants, there is increasing evidence that epigenetic variations are transmitted between generations, passing through the sex cells of successive generations. However, even in groups in which somatic cells cannot become germ-line cells, epigenetic variations that occur in the cells of the germ-line itself can be transmitted from generation to generation.

The important thing to realize about the epigenetic inheritance systems is that not only are cellular variants transmitted form one cell generation to the next, the generation of these variants is very often induced by the environment. Thus, whether or not a particular feedback system is turned on depends on environmental conditions; the way that a new form of prion first gets organized may depend on external conditions and be induced by them, and many variations in chromatin marks are induced by developmental and environmental conditions. The variations are not random. They are induced, and sometimes they are adaptive responses to the changed conditions. Adaptive epigenetic variations can be selected, accumulate, and be the basis for evolution at the cellular level.

Traditions in animals

We are all well aware of the fact that patterns of behaviour, preferences, ideas, and institutions are transmitted in human populations, forming typical traditions and cultures. In the human context it is also customary to talk about cultural evolution – for example, the evolution of technology, or of painting, or of local dialects. But man is not alone in being a "cultural" being. Groups of birds and mammals also have traditions that are based on information transmitted between generations of individuals through social learning – learning by example from other individuals. Of course, since non-human animals do not have symbolical representation and communication, there are important differences between animal traditions and human culture. However, it is very important to realize that non-human animals – notably birds and mammals – regularly transmit learnt information to each other, both within and between generations, and that this type of transmission may lead to new life-styles and new traditions. I shall illustrate this type of transmission through social learning with two examples: the transmission of novel feeding habits in Israeli black rats, and the transmission of food handling and other associated habits in the Japanese macaque monkeys in Koshima island.

The research on pine-cone opening behaviour by Israeli black rats is a beautiful illustration of a local animal tradition.[2] Israeli black rats have recently extended their range of habitats to include Jerusalem-pine forests. The major source of rat food in this habitat is the plentiful supply of

[2] Aisner R. and Terkel J. 1992. "Ontogeny of pine cone opening behaviour in the black rat (Rattus rattus)", *Anim. Behav.* 44: 327–336.

pine seeds, enclosed within pine-cones, growing on the upper branches of the trees. The pine seeds can be obtained only by using an elaborate pine-cone stripping technique. The results of a lengthy set of experiments have shown that black rat pups, but not adults, are able to learn the stripping technique by closely observing the partly stripped cones, and/or the cone-stripping behaviour of their mother, or any other experienced individual. The ability to strip pine-cones is the result of maternal transmission of behaviours, and not a novel genetic adaptation. Experimental cross-fostering of pups between experienced stripping mothers and “naive” (non-stripping) mothers has shown that pups learn from a skilful mother, irrespective of genetic relations.

The second example is probably the best-studied case of the establishment of local traditions in mammals. It was discovered by Japanese scientists who were studying Japanese macaques living on Koshima island, a wooded, precipitous mountain surrounded by sandy beaches and the sea.[3] To attract the macaques to an open space where they could observe their behaviour, the scientists scattered sweet potatoes along mountain trails and finally on the sandy sea shore. This innocent trick bore unexpected fruits. A particularly smart, female, Imo, then one and half years old, started washing the potatoes in a nearby stream, removing the soil from them before eating them. The new habit soon spread to other monkeys. Some time later, the potato washing habit begun to be performed in the sea, by the beach. Imo and other monkeys also bit the potatoes before they ate them, dipping them in the salty water, apparently to season them. The researchers on Koshima also threw wheat on the shore, expecting the macaques to spend a long time collecting the wheat grains from the sand, and expecting to be able to observe how they deal with such an unfamiliar type of food. However, the same Imo, now four years old, apparently an Einstein among macaques, found a way around that problem. Instead of picking up the grains laboriously one by one, she threw the mixed sand and wheat into the sea water; the heavier sand sunk into the sea and the wheat floated on the surface, allowing her to collect it promptly. The new habit spread slowly within the group, first from the young to the old, then from mothers to children. Old dominant male monkeys, entrenched in their old customs, and having less opportunity to interact with the young, failed to learn or were the last to learn. But the habit of bringing food to the sea had other effects. Infants carried by their mother to the sea became

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3 Kawamura S. 1959. “The process of sub-culture propagation among Japanese macaques”. *Primates*, 2: 43–45. Kawai M. 1965. “Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima island”. *Primates*, 6: 1–30.

accustomed to the water, and started playing in it. Swimming in the sea and even jumping and diving into it, became a popular habit, which in time became characteristic of the whole troop, including the adults. More recently, another new habit, eating raw fish, has begun spreading among the Koshima monkeys. This habit spread from peripheral hungry males to other members. The raw fish are not a favored food at all, but are now collected and eaten when there is nothing better around.

A whole new life style has developed. The original potato-washing tradition led to a direct elaboration of the pattern of behaviour – biting the potato to season it before dipping. But the main effects were indirect – it triggered another tradition of wheat scooping in the water, and the two food-washing traditions in turn triggered a tradition of swimming. Several closely interconnected habits, associated with the sea and the sandy beach, formed a new lifestyle. Each habit reinforces the others, since they are all associated with the new habitat and with the new habits related to it. Although there is not much modification in any single pattern of behaviour, the whole lifestyle has evolved by one modification in behaviour forming the conditions for the generation and propagation of another modification. The accumulation of modifications over time led to a whole lifestyle.

The new habits are not random variations – they are learnt responses to new conditions. They are transmitted from one generation to the next through various mechanisms of social learning. They accumulate and form complex new adaptations. Evolution has occurred through the acquisition and transmission of new behaviours.

The world of symbols

The ability to represent and transmit information in a symbolical form seems unique to human beings. Human language is a prime example – it is the major medium of information transmission in our species. I do not need to elaborate on the power of this type of representation and communication here, since, as scholars, we earn our living by using it. What is very clear is that this type of representation and communication sped cultural evolution enormously and extended it to new realms. Our species is the cultural species par excellence. The transmission of cultural variations, their selection according to complex individual and social criteria, and their accumulation are the basis of every aspect of our life: from eating food prepared according to multi-stage recipes to missile technology that enables us to send human beings to space. Cultural evolution is the major axis along which human evolution now proceeds.

The four systems of inheritance I have described (DNA, cellular, behavioural, symbolical) allow the transmission of information between biological entities at different levels of biological organization. They are not alternative to one another. As evolution proceeded, new inheritance systems and new modes of evolution were added to the previous ones. The generation of variation at these new levels is often not random. It is induced or learnt, and sometimes results in adaptive responses to new challenges. In the next section I argue that the evolution of these systems was part and parcel of the evolution of complexity.

Why is the evolution of systems leading to the inheritance of acquired variations inevitable?

When is it worthwhile to transmit acquired characters to the next generation? Under what kind of environmental and internal conditions? If we can define such environmental conditions and show that they are quite general and common and also show that the biological internal conditions are such that the origin of these new inheritance systems does not require unlikely modifications, then, given enough time, the evolution of new inheritance systems[4] is inevitable.

I cannot here go into the internal biological conditions that give rise to each of the new inheritance systems. However, I would like to briefly outline the kind of environmental conditions in which inheritance systems that transmit induced or learnt information are advantageous. I shall illustrate them with respect to the evolution of transmitting patterns of behaviour across generations through social learning.

Very generally, mechanisms allowing the transmission of induced or of learnt variations are advantageous if the environment has recurring features, but also has enough temporal or spatial diversity to preclude a fixed genetic response on the one hand, yet on the other hand make a response acquired by the individual through its own efforts too costly. Thus, learning from parents will be beneficial when individual learning by trial and error is time-consuming and dangerous and the environment changes so slowly that the information learnt from the parents is still relevant for the offspring. This means that changes last longer than the generation time of the organism, but not long enough for genetic fixation of the learnt response to occur. For example, if the availability of some food items such as seeds to seed-

[4] The origin of new inheritance systems is reviewed in: Jablonka E., Lamb M.J. and Avital E. 1998. "'Lamarckian' mechanisms in Darwinian evolution". *TREE*, 13: 206–210.

eating rodents varies every several rodent generations or periods of drought and cold last longer than the generation time of the individual animals experiencing them, socially transmitted behaviours can be advantageous. The best strategy for the naive individual is to learn the appropriate response from an experienced individual – to inherit the adaptive behavioral phenotype. The cost of individual learning is thus partially avoided.

The evolution of inheritance systems leading to the transmission of acquired variations is inevitable in the world organisms inhabit, where environmental fluctuations that are neither very short nor very long is common. The Israeli black rats and the Japanese macaques show us that such inheritance systems indeed do exist and play an important role in the lives of animals. However, until now we have treated the different inheritance systems as if they were isolated form each other, operating in parallel rather than interacting. In the short term, for a limited number of generations, this is useful, but the inheritance systems are not really isolated from each other. They interact and in the long term co-evolve. It is often necessary to understand how different inheritance systems and the variations transmitted through them affect each other to understand the evolution of a particular process or phenomenon. I shall illustrate this point with an example showing the co-evolution of genes and culture in human populations.

Multiple inheritance systems: a co-evolutionary perspective

There is a famous case that clearly illustrates one type of interaction and co-evolution between genes and culture: it is concerned with the evolution of the use of fresh milk as a source of food among adults in some human populations.[5] Fresh milk contains the sugar lactose, and the breakdown of lactose into its useful components (glucose and galactose) is accomplished by an enzyme, lactase-I, that all mammals are able to synthesize. The activity of this enzyme is normally very high in the young mammal after birth, but its activity decreases dramatically during weaning. Normally, therefore, fresh milk is digestible only during the suckling period. Adults outgrow their ability to digest the milk sugar because their lactase-I activity goes down. Consequently, when adults drink fresh milk, it does not yield much energy and often causes mild indigestion and sometimes diarrhea. This situation is characteristic not

[5] See Durham W. 1991. *Coevolution: Genes Culture and Human Diversity.* Stanford University Press. The case of the evolution of lactose absorption is reviewed on pp. 226–285.

only of non-human mammals, but also of most human populations. But there are some illuminating exceptions! There are adults who can break down lactose ("lactose absorbers") and hence benefit from drinking milk. A high proportion of these people is found in the dairying populations of North Europe and among wandering pastoralists (such as the Tutsi pastoralists in the Congo basin) who are totally dependent on fresh milk. It is much less common in other populations, including many dairying populations. How can we explain this rather odd distribution?

History and ecology provide the clues. The domestication of cattle led not only to the increase of eating beef, but also, about 4000–6000 years ago, to the use of fresh and processed milk products, such as cheese. With processed milk, there are no problems with lactose absorption, because the processing removes most of it. However, the wandering pastoralists of the Congo basin probably had difficulties finding the opportunity to process milk and so came to depend heavily on fresh milk as a ready food source. Adults needed the ability to digest the lactose in this milk. Those with the genetic ability to do so thrived and reproduced, and the gene or genes responsible spread through the population.

What about the other, non-wandering populations with adults who can absorb lactose? It happens that lactose, the sugar found in fresh milk, is not only an excellent energy source, but also acts like a vitamin D supplement, facilitating the absorption of calcium. This is of great importance in environments where there is a deficiency of vitamin D and hence of calcium. People living in sunny areas have a constant supply of vitamin D, because solar radiation converts precursor steroids to vitamin D. But in regions that receive little sunlight, vitamin D may be in short supply. If so, the ability to absorb lactose after weaning has a great advantage, because it supplies vitamin D and prevents the development of rickets, a crippling softening of the bones resulting from calcium deficiency. Consequently, in cultures that use cattle and live in regions with little solar radiation, individuals who are able to absorb lactose as adults have an advantage over non-absorbers. We can therefore expect such individuals to leave more descendants and in time to become the majority in the population. The distribution of lactose absorbers fits this expectation – their frequency is particularly high in populations living at high latitudes with little sunlight.

The increase in the frequency of the genes enabling adults to make good use of fresh milk is therefore the result of a cultural change, the domestication of cattle. Domestication was beneficial for individuals in all communities in which it was practiced, because beef and milk are energy-rich foods. However, in some populations, such as those of the wandering pastoralists and the populations of Northern Europe, fresh milk became important. It is in these populations that we see not only a high frequency of lactose absorbers, but also a high cultural regard for fresh milk. In the creation myths of the Indo-European people, the importance of the bovine, and especially of the female cow as a source of fresh milk, increases the higher the latitude! In the myths of the most northern populations, the first animals to be created are female cows, who produce a lot of milk. This milk is drunk fresh by giants and gods and is considered to be the source of their great size and strength. The first bovine of creation was not used for food or sacrificed, but continues to nurture the world.

So the domestication of cattle, a cultural event, led to new evolutionary opportunities. The continuous availability of culturally harvested fresh milk gave, in some dairying populations, an advantage to the few adults who were able to absorb lactose. They were healthier and their reproductive success was greater. The benefits of milk drinking led to the glorification of milk: myths developed that reflected the importance of fresh milk, and at the same time reinforced and encouraged its consumption, leading to stronger selection for lactose absorbers; the increase in the frequency of adult lactose absorbers further enhanced the "educational" value of the myth. A positive feedback loop between genetic and cultural evolution was thus formed. Culture and genes co-evolved, positively affecting one another.

Conclusions

The transmission of information between generation of organisms occurs at several levels of biological organization – the level of the genetic material, the cellular level, the behavioural level, and the symbolical level. At each level, the generation of variations in the transmitted information can be either accidental and "blind" with relation to the environment affecting this level, or it can be "directed": the variation is induced or learnt and is a non-accidental, often adaptive response to environmental conditions. This is very apparent when we look at non-DNA inheritance system, but even the DNA system is more complex and sophisticated than once believed, and some genetic variation seems guided or directed.

All the systems of inheritance evolved by natural selection, which may often have involved accidental variations. The conditions in which the inheritance of acquired variations is advantageous are common, and the evolution of systems allowing the production of non-accidental, learnt, or induced variations is therefore inevitable. With the emergence of new inheritance systems, evolution can occur at different levels of biological organization. As I have tried to show, there are interactions between the different levels, and it is necessary to consider these interactions to understand observed traits and behaviours, including traits and behaviour patterns in our own species. The attempt to derive all evolutionary adaptations from considerations based on genetic evolution and gene selection alone is therefore doomed to failure. Similarly, the attempt to ignore genetic (or epigenetic) evolution and explain all human cultural processes and products at the cultural evolution level alone can yield only partial understanding. An integrative approach, considering all inheritance systems and weighing their relative importance in any particular case is necessary.