REVIEW ARTICLE

A comparison of biological and cultural evolution

PETTER PORTIN*

Laboratory of Genetics, Department of Biology, University of Turku, FI-20014 Turku, Finland

Abstract

This review begins with a definition of biological evolution and a description of its general principles. This is followed by a presentation of the biological basis of culture, specifically the concept of social selection. Further, conditions for cultural evolution are proposed, including a suggestion for language being the cultural replicator corresponding to the concept of the gene in biological evolution. Principles of cultural evolution are put forward and compared to the principles of biological evolution. Special emphasis is laid on the principle of selection in cultural evolution, including presentation of the concept of cultural fitness. The importance of language as a necessary condition for cultural evolution is stressed. Subsequently, prime differences between biological and cultural evolution are presented, followed by a discussion on interaction of our genome and our culture. The review aims at contributing to the present discussion concerning the modern development of the general theory of evolution, for example by giving a tentative formulation of the necessary and sufficient conditions for cultural evolution, and proposing that human creativity and mind reading or theory of mind are motors specific for it. The paper ends with the notion of the still ongoing coevolution of genes and culture.

[Portin P. 2015 A comparison of biological and cultural evolution. *J. Genet.* **94**, 155–168]

Introduction

As long ago as 1871, Charles Darwin considered whether the intellectual and moral characters of man have emerged as results of biological selection in manner similar to anatomical and physiological characters (Darwin 1913, pages 195–224). In this way, he was the first to present a hypothesis of the biological basis of culture.

In a series of influential and pioneering publications, the American philosopher of science David L. Hull has, together with his coworkers, argued in favour of the view that they call generalized Darwinism. By this is meant that the general principles of Darwinism apply not only to biological evolution but also to evolution of societies and culture (Aldrich *et al.* 2008; Hull 1988, 2001a; Hull *et al.* 2001). According to these authors, Darwinian ideas have important implications for social scientists concerning rationality and psyche of human agents. Assumptions concerning human agents must be consistent with our understanding of human evolution. Darwinian evolution involves development, retention and selection of information concerning adaptive solutions to survival problems faced by organisms in their environment. With regard to evolution of societies and culture, Darwinism by itself is insufficient to provide full and complete answers, but it provides a general framework in which additional and context-specific explanations may be placed.

One of the most remarkable evolutionary theorists of our time, the American Richard C. Lewontin, has suggested that biological evolution of species as well as development of individuals occur as a result of a complicated interaction of genes, individuals and environment, forming what could be termed a triple helix (Lewontin 2000). Individuals themselves are thus active actors both in their own development and in evolution of the species. In other words, activity of the individual itself plays a part in development of the phenotype.

With respect to activity of the individual itself, cultural traits, such as cognition, the faculty for the processing of information, applying knowledge, and changing preferences, and other mental capacities, such as learning, thinking and emotions, are in a central position. Of these, learning can be defined as the act of acquiring new, or modifying and reinforcing, existing knowledge, behaviours, skills, values or preferences. Concerning the significance of environment for development of different mental capacities, richness of the environment is important. This has been shown with experiments on behavioural or environmental enrichment, providing the experimental subjects with environmental stimuli that improve psychological and physiological well-being (Rampon *et al.* 2000). It is worth noting that both learning

*E-mail: petter.portin@utu.fi.

Keywords. fitness; information; language; learning; teaching.

(Cavallaro *et al.* 2002) and environmental enrichment (Rampon *et al.* 2000) alter gene transcription in the brains of young animals. Pathways of gene functions influenced by these experiences include cell-survival-associated genes and genes involved in synaptic plasticity. Thus, it seems that there is a positive feedback loop between learning and the genes associated with it.

In conclusion, human biological evolution and evolution of human culture are, so to speak, the result of teamwork between genes, individuals, biotic and abiotic environment, and the culture constructed by man, figuratively speaking a quadruple helix. The aim of the present study was to describe the nature of this biological and cultural evolution and to provide a suggestion for their comparison, in other words to elucidate the nature of this quadruple helix.

What is biological evolution, and what is cultural evolution?

Biological evolution is a population-level process guided in large part by selection and, in small populations, also by random processes. In the biological world, there are two types of selection targeted at individuals and based on differences in their genes. These types of selection are natural selection, described by Charles Darwin in 1859 (Darwin 1968), and sexual selection, also described by Darwin (1913).

In the theory of evolution, the concept of 'fitness' is central. 'Fitness' is the relative capacity of the individual to produce fertile offspring, or to have its genes represented in the gene pool of the next generation. In general, fitness is constituted of two components, the survival component and the reproduction component. To be fit, an organism must survive until reproductive age and then reproduce. In addition to this, many animals, notably several birds and all mammals, man included, possess a third component of fitness, which may be called a 'fostering' or 'nursing' component. By this it is meant that these animals, to be fit, must foster their offspring until they reach reproductive age.

Culture can be defined as the wholeness of the mental and material achievements of a society or mankind as a whole. The influential American anthropologist Adamson Hoebel describes culture as an integrated system of learned behaviour patterns that are characteristic of members of a society and are not a result of biological inheritance (Hoebel 1972), to which, however, it must be added that, according to the modern view, genes and learning are not independent elements as cultural factors.

Cultural evolution provides an explanation for how cultures and societies change over time. Whereas cultural development relies upon processes that tend to increase complexity of a society or culture, cultural evolution also covers processes that can lead to a decrease in complexity of culture, or that can produce variation or proliferation without any seemingly significant changes in the complexity. Cultural evolution can be defined as the 'process by which structural reorganization is affected through time, eventually producing a form or structure which is qualitatively different from the ancestral form' (see e.g. Korotayev 2004).

In biological evolution, two processes that act on different levels can be distinguished: microevolution and macroevolution. It seems to me that a parallel can be drawn from cultural evolution to biological microevolution—though less so to biological macroevolution. It also seems that researchers of the topic are rather united regarding the hypothesis that cultural evolution in general mainly obeys the same regularities as biological evolution, although considerable differences exist.

General principles of evolution

Cultural evolution follows Darwinian principles as biological evolution was first presented by the Italian population geneticist Luigi Luca Cavalli-Sforza and the Australian-American geneticist Marcus W. Feldman in 1981 (Cavalli-Sforza and Feldman 1981).

These principles are those of variation, inheritance and selection. These principles, which can also be called the postulates of the theory of evolution, are the necessary conditions for biological evolution, and together they also constitute a sufficient condition for it (Lewontin 1970, 1982 pp. 149). If these principles are in force, biological evolution necessarily follows.

The principle of variation means that all organisms are variable in such a way that in nature no two identical individuals can be observed. The principle of inheritance means that at least a part of the variation is hereditary in such a way that related individuals resemble each other more than other individuals of the population on average.

The theory of biological evolution does not include inheritance of acquired characteristics, and, on the basis of empirical evidence first presented by the German evolutionary biologist August Weismann originally in 1891 (Weismann 1892, 1893), the very existence of inheritance of acquired characters is denied.

The principle of selection, which Charles Darwin first realized and then published in his book *On The Origin of Species* in 1859 (Darwin 1968), means that those individuals best adapted to the environmental conditions produce more fertile offspring than other individuals. If the adaptation is at least partly hereditary, it follows that the mean of the adaptation of the population increases as long as there is variation in it. This principle was formulated by the British statistician and evolutionary biologist Ronald A. Fisher in the Fundamental Theorem of Natural Selection in 1930 (Fisher 1958).

Fisher's theorem (FTNS) seems to be, however, limited to single-locus models only, and, moreover, it focusses on partial change in the mean fitness rather than total change, i.e. that component of the change in mean fitness ascribed by Fisher to changes in gene frequency (Ewens 1989). Therefore, the theorem has since been developed to concern more general cases, for example by Warren J. Ewens, Steven A. Frank and, above all, the American population geneticist George R. Price.

First, Ewens (1969a, 1969b) generalized the theorem to apply to many loci. Then, Price (1972b) showed that Fisher's theorem was mathematically correct as stated, but not of great biological significance. Already before this, Price (1970, 1972a) had published his famous generalization of FTNS known as the Price equation. The equation gives gene frequency change under selection from one generation to the next for a single gene or for any linear function of any number of genes at any number of loci. Subsequently, Ewens (1992) put forward an optimizing principle of natural selection stating that 'of all gene frequency changes which lead to the same partial increase in mean fitness as the natural selection gene frequency changes, the natural selection values minimize a generalized distance measure between parent and daughter generation gene frequency values' (Ewens 1992 pp. 333). Frank (1997), for his part, presented a general framework, based on the Price equation, to unify different models of natural selection.

The prevailing formulation of the theory of biological evolution is called neo-Darwinism, or the synthetic theory of evolution, so called since it involves a synthesis of genetics and Darwinism, the theory of evolution formulated by Darwin. In nature, not one single fact has been observed that is in contradiction with this Darwinian theory of evolution. In recent years, however, facts have been observed that have not yet been incorporated into the present synthetic theory of evolution. This does not mean that the theory is erroneous, but that the theory must be supplemented to assimilate the new findings.

Perhaps the most important of those observations that are not currently incorporated in the synthetic theory of evolution is transgenerational epigenetic inheritance, or the inheritance of acquired states of the function of genes from one generation of individuals to the next (see e.g. Portin 2012). Consequently, evolutionary biologists have begun to present opinions that suggest the need for a new synthesis of evolutionary theory. Without doubt, a new synthesis is necessary, and it has even been given a name: it is called the Extended Evolutionary Synthesis (Pigliucci 2007).

The biological basis of origin of culture

Implications of environmental factors in evolution of human culture

Before dealing with genetic evolution of culture, it is necessary to briefly discuss the significance of ecological and other environmental circumstances for origin and development of human culture, recently reviewed by Daniel Nettle, for example (Nettle 2009). It is almost self-evident that a supply of fresh water and food, and, consequently, suitable ecological and climatic conditions for food production and yield of water, were necessary for the birth and development of human culture (see e.g. Deevey 1960). It is also clear that supply of raw materials for building houses and other dwellings, as well as for making different tools and other necessities, is significant for human culture. These conditions for culture have led to two facts: firstly, that mankind has been able to inhabit, practically speaking, all areas on the continents and islands on Earth that are free of glaciers, and, secondly, that the distribution of our species is limited to these areas.

The problem of evolution of cooperation and its different solutions

The origin and evolution of unquestionable animal cooperation has constituted a difficult problem for the theory of evolution. This is because the starting point of the theory of natural selection is that individual animals tend to behave selfishly in order to maximize their own fitness. Specifically, evolution of colonies of eusocial Hymenoptera such as bees and ants, based on altruistic cooperation, already constituted a twisted problem for Charles Darwin. In these colonies, individuals of the worker caste abandon their own reproduction and instead help the queen of the colony to produce offspring. Darwin's own solution to this puzzle was that he regarded the whole colony as a kind of a superindividual and, as such, the unit of natural selection. This solution, however, is an unsatisfactory *ad hoc* hypothesis.

The solution to the puzzle of the evolution of eusociality was recognized by the British evolutionary biologist William D. Hamilton in 1963 and 1964 (Hamilton 1963, 1964). This solution bears the name Hamilton's rule, or 'kin selection'. The model explains that cooperation, or in this case the helping of other individuals to reproduce, is cost-effective in the evolutionary sense if the costs of the social behaviour for the fitness of the helper are lower than the benefits for the fitness of the helped caused by it. In other words, expressed briefly, according to this hypothesis the solution to the evolution of sociality is that by assisting kindred individuals to produce offspring the socially behaving individual simultaneously increases the frequency of genes identical with the individual's own genes in the population. This measure of fitness is called 'inclusive fitness' of the individual in question. This means that a certain part of the fitness of kindred individuals, determined by the degree of kinship and the amount of help given by the individual, will be included into the fitness of the helping individual in question.

As noted by Boyd and Richerson (1989), for example, explanations of cooperation based on kin selection are dependent on direct interactions of genetically related individuals, whereas cooperation in human societies often occurs between genetically unrelated individuals, which fact seems to preclude explanations based on direct reciprocity. A solution to this problem was, however, suggested in 1971 by Robert L. Trivers, an American evolutionary biologist and sociobiologist in his theory of reciprocal altruism (Trivers 1971).

The theory of reciprocal altruism explains how certain classes of behaviour conveniently denoted as altruistic can be selected for even when the recipient is so distantly related to the organism performing the altruistic act that kin selection can be ruled out. Thus, the model will apply even to altruistic behaviour between members of different species. Under certain conditions, natural selection favours these altruistic behaviours because in the long run they benefit the organism performing them.

The idea of the model of reciprocal altruism, argued mathematically by Trivers (1971), is that it is beneficial for an organism to act in an altruistic manner that temporarily reduces its fitness while increasing another organism's fitness with the expectation that the other organism will act in a similar manner at a later time. In addition, Stephens (1996) showed a set of four necessary and jointly sufficient conditions for an instance of reciprocal altruism, as well as two additional conditions necessary for reciprocal altruism to evolve.

While the theory of reciprocal altruism mainly deals with cooperation between individuals, cooperation in human societies often occurs between groups. A model aiming at an explanation of cooperation between human groups has been put forward by the American biologist Richard D. Alexander (Alexander 1987). He proposed that large-scale cooperation among humans can be understood as resulting from networks of indirect reciprocity. However, it was Trivers's article that provided the basis for further accounts of indirect reciprocity and evolution of such complex phenomena as moral systems and ethics, for instance, later discussed by Alexander (1987).

Inclusive fitness has been widely accepted as a general method to explain evolution of social behaviour. Adherents of the theory even claim that it is as general as the theory of natural selection itself. Recently, however, the reliability of this claim has been disputed. Eminent scientists have demonstrated that inclusive fitness is a limited concept, and the necessity of the theory as a whole has been questioned (Allen *et al.* 2013). According to these scientists, the claim in question is based on using linear regression to split an individual's fitness into components due to self and others, a regression method they found to be useless for prediction or interpretation of evolutionary processes, and this regression method weakness was found to limit the validity of inclusive fitness theory in general (Allen *et al.* 2013). At this point, it should also be mentioned that according to studies by Simon (2014), contrary to the opinion of many researchers in the field, the theories of kin selection and group selection are not mathematically equivalent. This result seems to imply that group selection models of cooperation cannot be derived from individual-centred kin selection models, but a group-centred view must be adopted.

With regard to evolution of social behaviour and the theory of inclusive fitness, it should also be stressed that, contrary to the expectations of the theory of inclusive fitness, helping to reproduce also occurs between individuals that are entirely unrelated. Such is the case, for example, in the symbiotic relationships between individuals belonging to different species, and, for instance, in the pollination of plants by bees. In the explanation of this kind of social relationship, the principle of reciprocal altruism described by Trivers (1971), and the different game-theoretical models based on it, seem to be relevant.

In this context, the conclusion reached by Fletcher and Zwick (2006) seems to be very important. They showed that, contrary to the earlier understanding, the theories of inclusive fitness and reciprocal altruism are not to be seen as distinct explanations for how altruism evolves as they can in fact be united. According to these two researchers, inclusive fitness and reciprocal altruism actually rely on the same underlying mechanism, which was analysed by employing David C. Queller's generalization (Queller 1992) of Hamilton's rule.

Game-theoretical models also seem to apply to the explanation of problems concerning the stabilization of cooperation related to modern democracy in human societies (Hilbe *et al.* 2014). Here it is interesting to note that according to the computer simulation studies of Wang *et al.* (2014) on the evolution of cooperation between different populations, links to other populations outside the immediate community promote cooperation, a result that seems to be particularly applicable to human societies, where an individual is typically a member in many different social networks.

Even the game-theoretical models mentioned, however, are insufficient for explanation of human ultrasociality; therefore, a hypothesis concerning a completely new form of selection, namely social selection (Nesse 2009), is needed. It seems that gratuitous altruism or the ability and need to help other individuals, be they of one's own or of a different species, without benefit for the fitness of the helper, belongs to human sociality.

Social selection and origin of culture

We are naturally curious to know what occurred in our evolutionary history that made us capable of culture. This sequence of events clearly involved so many mutually interacting factors and cycles of repeating causes that their description necessarily simplifies the incidents themselves. Old suppositions that have comprehended biological evolution and cultural evolution as separate and alternative phenomena have been replaced by new explanations that emphasize their reciprocity. Biological selection creates capacities that make culture possible, and culture has produced new selection operators that have an effect on our biology.

Different selection operators have given rise to many characteristics in our species associated with culture. These are, for example, erect walking on two feet, hunting, speech, construction of tools, handedness (handedness is not specifically human: many primates, even elephants show it), agriculture, cooperation, emotions, facial expressions, the ability to anticipate things or the ability to foreshadow the future, imitation, social learning, empathy, morality, and the theory of mind, by which is meant the individual's comprehension that other individuals, too, have their own consciousness, thoughts, emotions and feelings. Many biological selection factors have been proposed as explanations for the origin of these characteristics. These include, for example, sexual selection, kin selection and different forms of group selection. Even together, however, these forms of selection do not seem to be sufficient as an explanation for emergence of human ultrasociality. Therefore, social selection has been suggested as a process capable of explaining, at least partly, the evolution of human social characteristics (Nesse 2009). On the other hand, however, natural selection and sexual selection are also sufficient to explain certain aspects of human behaviour.

Social selection is, in addition to natural selection and sexual selection, a third form of selection operating in biological evolution. Natural selection involves competition between individuals for ecological resources, and sexual selection involves competition for sexual partners. Social selection on its part comprises competition for other social resources than the members of the opposite sex. In social selection, an important role is played by different aspects of positive and negative feedback given by members of the social group in which the individual in question lives. Therefore, in practice, in social selection the act of selection is performed by other individuals than the one whose fitness will be affected by the selection. In this respect, social selection thus clearly differs from sexual selection proper. To provide an example, generosity is a target of positive social selection in human societies.

Social selection is a very important candidate in the search for an explanation for ultrasociality, so typical of the human species, surpassing the circle of kindred individuals; therefore, it is regarded as a significant factor in emergence and evolution of human culture. (Biological social selection, which involves the biological fitness of individuals, must not be confused with the corresponding concept in sociology, which means the overepresentation or underrepresentation of certain kinds of individuals in a given social group, such as overrepresentation of tall people in a basketball team.)

The theory of social selection was first presented in its entire breadth by the American theoretical biologist Mary Jane West-Eberhard in two papers in 1979 and 1983 (West-Eberhard 1979, 1983). She defined social selection as a super-type of sexual selection—social competition for any kind of resources that affect choice of the mating partner, not only as competition for members of the opposite sex as such.

According to West-Eberhard (1979, 1983), social selection can have an effect on the evolution of characteristics that make the individual more attractive as a social partner. These characteristics include, firstly, possessing resources such as good health and vitality, desirable personal capabilities, influential confederates and a powerful social status. Secondly, they include an inclination to distribute one's own resources faithfully and selectively with social companions. Thirdly, these characteristics also include the ability to have a feeling about what other individuals expect from a companion, and fourthly, a strong motivation to please companions and other members of the social group. Certainly, these characteristics can be favourable in sexual selection, too.

Of course, these characteristics do not yet constitute culture, but they make the human species capable of creating and embracing culture. Evolution of culture began only after the cognitive and emotional skills required had evolved. Social selection offers an explanation for the presentation of social resources and generosity, both of which are typical of every culture (West-Eberhard 1979, 1983).

Thus, in the early stages of the evolutionary history of our species, social selection would have been able to create the conditions for development of culture by giving rise to such necessary conditions for culture as genuine altruism in individuals and the ability to cooperate.

While culture cannot be explained solely on the basis of natural selection, sexual selection and social selection, it, nevertheless, seems probable that of these forces social selection played an especially important role at the turning point of the evolution of mankind when culture became possible. As soon as culture had come into existence, social selection became a selective factor in its own right. It was then able to create more and more complex social skills which in turn led to development of more and more complex forms of culture. In this way, the mutual teamwork of genes, individuals, environment and culture, the self-sustaining quadruple helix of biological and cultural evolution, was born.

What is cultural evolution?

Cultural evolution, or the development of cultures, can be defined as change of the behaviour of individuals through learning in an individual from another. In this case, selection is targeted at any behavioural characteristic. In humans, cultural selection is at least partly based on conscious action. In cultural evolution, selection is not, at least directly, targeted at the genetic information included in the DNA, but at that information that is produced by the human species itself, which can be material or immaterial.

It seems that cultural evolution is Darwinian in the sense that its necessary conditions are the principles of variation, inheritance and selection. In the cultural form of evolution, however, these principles occur in far more complex forms than in the biological. In addition, these are not the only necessary conditions for cultural evolution, since the sufficient conditions for cultural evolution include several other necessary conditions, all of which are probably not even known yet. The concept of fitness, so central in biological evolution, seems not to apply as such to cultural evolution, and, further, the levels of selection in cultural evolution are far more complex than in biological evolution.

Conditions for evolution of culture

As in biological evolution, the necessary conditions for development of culture include variation, inheritance and selection. In addition to these, the necessary conditions for cultural evolution are at least storage, collection and accumulation of information, formation of social groups, work and division of labour between individuals, the subsequent development of society, and spoken language.

Regarding the conditions for culture, it is necessary to distinguish between animal social systems and human culture, because at least the first four conditions mentioned can also be observed in many animal societies; spoken language, however, is a clear exception. The partial similarity of animal social systems and human culture, on the other hand, indicates that development of human culture is associated with our biological evolution and origin.

In addition to the list above, there are most likely yet other necessary conditions for development of human culture, though of course it is also possible that the five conditions mentioned here together form the sufficient conditions. The discovery of all necessary conditions for cultural evolution naturally is very important for formulation of a theory of cultural evolution.

What in cultural evolution corresponds to the concept of the gene in biological evolution?

For the principles of variation, inheritance and selection to be true in cultural evolution, some form of a concept corresponding to the concept of the gene in biological evolution is needed–a unit that is variable, is transferred from one generation to the next, and on which selection is based. Consequently, such a unit must be one that is able to copy itself, a replicator.

In his book *The Selfish Gene*, first published in 1976, the British evolutionary biologist Richard Dawkins proposed the concept of the 'meme' for such a cultural replicator (Dawkins 2006). (The word meme has been derived from the word *mimesis* in Greek, meaning imitation.)

The meme is defined as a cultural and communicational replicator. Dawkins provides an explanation for the word meme as follows: 'We need a name for the new replicator, a noun that conveys the idea of a unit of cultural transmission, or a unit of *imitation*.' As examples of memes he lists tunes, ideas, catch-phrases, clothes fashions, and ways of making pots or of building arches (Dawkins 2006 p. 192).

According to Dawkins, both genes and memes are selfish, in one sense independent entities that use humans as vehicles of their own propagation. Genes build organisms for their living media, and the successful reproduction of these biological constructs ensures the transmission of genes from one generation to the next. Memes, too, are selfish entities using humans as means of transportation for their own propagation. Memes, which have an independent life of their own, compete for space in the human minds.

Later, Dawkins distanced himself from the concept he created. He has admitted that the replication process of memes is far more inaccurate than that of genes (Dawkins 1982). In addition, memes, in contrast to genes, may become partly mixed with each other. This makes the idea of the parallel nature of genes and memes troublesome.

In my view, the understanding of memes as units of cultural evolution simplifies the entire phenomenon excessively. In addition, the definition of memes as self-sufficient entities is in contradiction to the fact that memes cannot live a life independent of human beings and the entirety of the culture created by mankind. The idea of humans as a passive culture medium or substrate for memes entirely neglects the fact that in essence human beings are rational actors. On the other hand, however, the learning of behavioural habits also involves irrational features: specifically the learning incidents of children are at least partly based on imitation. In these contexts, use of the concept of the meme seems to be justified.

A better candidate for the replicator would, in my view, be *language* in the broad sense of the word, an opinion shared with the British evolutionary biologist Mark Pagel, who presented it while discussing development of human languages (Pagel 2009).

According to Pagel, language has many features resembling genetics, and development of languages can very well be compared to biological evolution. For example, both contain discrete elements of heredity. These are genes in biological evolution, and words and phonemes in development of languages. In development of languages different innovations, such as new words and tones of voice, for example, correspond to mutations in biological evolution. Further, according to Pagel, in development of languages communal preferences and trends correspond to natural selection in biological evolution. An analogy can also be seen between regional variation in organisms and dialects of languages and their chains.

The principle of variation in cultural evolution

Variation is a necessary condition for all selection-based evolution because nothing can be selected from homogeneous material. In biological evolution, the sources of variation are the phenomenon of mutation and genetic recombination. The sources of variation in the realm of cultural evolution are also rather easy to identify. In short, they are firstly innovations and discoveries, and secondly construction and composition. These can be seen as the counterparts of mutation and genetic recombination, respectively, in biological evolution.

The principle of inheritance in cultural evolution

Since both biological and cultural evolution require transfer of information, the principle of inheritance is a necessary condition for both types of evolution. In cultural evolution, inheritance is a sequence of events in which information is transferred from one individual to another with the aid of social learning mechanisms. These are imitation, learning and language (Mesoudi and Whiten 2008).

In contrast to biological evolution, in which the transfer of information in the context of inheritance is based on genes and is in man unidirectional and vertical, the mechanism of inheritance in cultural evolution is firstly social, conceptual and mental, and secondly bidirectional vertically, horizontally and obliquely, in other words network-like. Further, information transfer in cultural evolution can often be indirect, mediated from key individuals in the social group, or frequency dependent, derived from individuals representing the majority in the group (Feldman and Laland 1996) (figure 1).

In addition, also in contrast to biological evolution, acquired characteristics are heritable in cultural evolution. Further, while in biological evolution genetic information is received only once during an organism's lifetime at conception, information in cultural evolution is received throughout life. Thirdly, information in biological evolution proceeds slowly and only via generational changes, whereas in cultural evolution information can move very rapidly. Consequently, cultural evolution is far more rapid than biological evolution. Fourthly, in biological evolution, an individual cannot have any influence on the content of genetic information he or she receives, but in cultural evolution the individuals can choose the information that they accept.

Thus, there are significant differences between biological and cultural evolution in the realization of the principle of inheritance. This is sufficient reason to see biological and cultural evolution as partly separate phenomena (Strimling *et al.* 2009) even though they are tightly intertwined.

The principle of selection in cultural evolution

It is almost undisputed that, essentially, selection, be it natural selection, sexual selection, social selection or selection within the realm of culture, is the only means of establishing new information in a population. As a result, selection is a necessary condition for both biological evolution and cultural evolution. However, it appears that when natural selection and sexual selection are unconscious material processes based on fitness differences between individuals, selection within the domain of cultural evolution is eventually always more or less conscious. Further, it seems that in the realm of cultural evolution, the targets of selection can be groups of individuals in addition to separate individuals because culture is essentially a group phenomenon and cannot be born in a single individual.

Similarly, individuals can neither adopt culture nor carry out preferences within it without being members of a social group inside which they spread and accept information. As a consequence, the birth of the social group and the subsequent formation of society are necessary conditions for development of culture.

A very good example of the power of selection in evolution of culture is development of science. In this regard, David L. Hull and Robert J. Richards, an American historian of science, have made successful attempts to analyse this issue (Hull 2001a, 2001b; Richards 1977, 1987). While studying how cultural evolution works in practice, they demonstrated how development of science can be analysed as a selection process. A single scientist solving an important problem makes science look very efficient. Treating science as a selection process, however, casts it in a very different light. From the selective perspective, science as a process involves production of numerous alternatives and a selection among them, and this perspective explains why science is as successful as it is (Hull 2001b).

The British sociologists Claire and W. M. S. Russell have, in their studies concerning the cultures of apes, created the concept of behavioural selection, by which they mean that changes of culture occur as consequences of changes in the behaviour of individuals (Russell and Russell 1989). Reciprocally, changes in culture lead to changes in the behaviour of the individuals.

Changes in behaviour occur through learning and imitation. Therefore, behavioural selection is a better proposal for the mechanism of selection in cultural evolution than meme selection, which, of the forms of learning, in actual fact takes only imitation into account, and considers individuals only as passive living media of the memes. Behavioural selection, in contrast, includes all forms of learning, and considers

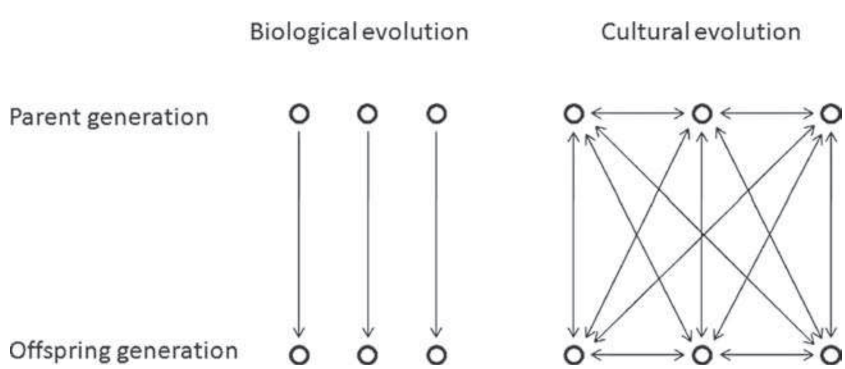

Figure 1. Transfer of information in biological and cultural evolution. In biological evolution, the transfer is unidirectional and vertical, whereas in cultural evolution it is bidirectional, and vertical, horizontal and oblique—in other words, network-like. In addition, information transfer in cultural evolution is often indirect, being mediated from key individuals in the social group, or frequency dependent, derived from individuals representing the majority in the group (Feldman and Laland 1996).

individuals to be active cultural actors. Further, in the model of behavioural selection, the hypothesis of language as the unit of cultural evolution can be included.

The motor or driving force of biological evolution is the interplay between heritable variation and selection caused by changes in environmental circumstances. The question then logically follows: does cultural evolution have its own motor? It seems that the interaction between creative activity of individuals and expectations of society, connected with behavioural selection, may be such an operator. Creativity, the process of producing something that is both original and worthwhile (Davidson and Sternberg 2003), is a characteristic of a given individual and yet is tightly connected to society and the historical situation in which the individual lives. From this it follows that variation in creativity between unique individuals, and between the unique histories of their societies, can quite possibly explain cultural differences among groups.

In addition to creativity, another characteristic, possibly specific only to humans and which is an important driving force for cultural evolution, is the theory of mind, or mind reading, recently reviewed by Cecilia M. Heyes and Chris D. Frith (Heyes and Frith 2014). It can be defined as the ability to attribute different mental states to oneself and others and to understand that others have mental states that are different from one's own. Mind reading allows us to predict, explain, mold and manipulate each other's behaviour in ways that go well beyond the capabilities of other animals; therefore, mind reading is crucial to understanding what it means to be human (Heyes and Frith 2014).

In biological evolution, success of individuals is described with the aid of the concept of fitness. It is a simple index that measures reproductive success of individuals. The question arises whether a corresponding success index appears in cultural evolution.

The concept of 'cultural fitness' has been proposed as such an index by the American biological anthropologist William H. Durham (Durham 1982). Cultural fitness is defined as a function of time. The longer the period of time that a cultural characteristic is preserved and transmitted from one individual to another in the population, the better its cultural fitness.

The concept of cultural fitness must, however, be regarded as too simple due to the fact that preservation of a cultural trait is dependent on the number of learning chances an individual has to adopt the trait. At the same time, it has been proposed that the course of cultural evolution can be predicted precisely on the basis of number of repeats of the learning event in the population, regardless of mode of transmission, be it vertical, horizontal or oblique, and a mathematical model has been constructed for a success index within the realm of cultural evolution (Strimling *et al.* 2009).

In this model, the competitive ability of different variants of culture is described with the aid of two variables, the value of which can vary between zero and one. These variables are the diffusion potential (d) and the retention potential (r). The former variable summarizes the properties of a cultural variant that make it likely to be acquired by new individuals, and the latter describes the potential of the variable, when held by an individual, to resist being replaced. As one illustrative example of the model, the authors give the following: consider competing consumer products. Throughout life, people will have multiple opportunities to learn about various products and, possibly, try them. As studied in consumer psychology, the products that people try will be determined by certain factors (e.g. commercials), whereas different factors (e.g. satisfaction) will determine the products that people will continue using. The values of d and r would summarize the former and latter factors, respectively (Strimling *et al.* 2009).

By using only these two variables the Swedish researchers cited above have created a mathematical model for the significance of repeated learning with regard to the principle of selection in cultural evolution (Strimling *et al.* 2009). Learning and teaching are ways of behaviour. Consequently, for the time being, behavioural selection, in the broad sense of the concept, can be regarded as the best proposal for the mechanism of selection in cultural evolution. Its main principle is simply the following: changes in behaviour of individual members of a population lead to changes in the culture of that group of individuals, and, reciprocally, changes in culture lead to changes in behaviour of individuals. The groups themselves also practise cultural competition among themselves, and, consequently, ultimately both individuals and groups formed by them are targets of selection in cultural evolution.

A good example of cultural competition, which has also been mathematically modeled, is the phenomenon of language competition, which is the situation when multiple languages come into contact with each other, and one or more of them may become endangered as speakers may prefer using others (Zhang and Gong 2013). Such competition can be viewed as a process in which languages gain a survival advantage via resource plunder. Resource here refers to the speakers in the competing region, and survival advantage of a language manifests itself primarily in its number of speakers in this region, and the competition dynamics are reflected mainly through change in population sizes of the languages in this region (Zhang and Gong 2013). All learning and teaching is based on interaction of individuals, and individuals make choices on the basis of what they have learned. Among other things, these facts also indicate the hierarchical and complicated nature of selection in cultural evolution. In this regard, cultural evolution differs from biological evolution, in which the levels of selection are far simpler and most often can become reduced to individual selection.

Social group selection is important in cultural evolution

Compared with most other species, humans cooperate on a very large scale and act in concert to achieve common goals. The scale of human cooperation is difficult to explain in terms of choice by self-interested actors, i.e. on the basis of individual selection. The simplest way to explain the scale of human cooperation is to assume that humans are not solely self-interested, but in making choices individuals balance changes in their own welfare against changes in the welfare of others. With their coworkers, the Americans Peter J. Richerson, a biologist, and Robert Boyd, an anthropologist, have developed a series of models of human cooperation, which demonstrate the feasibility of such group selection in cultural evolution (Boyd and Richerson 1981, 1982, 1985, 1989; Soltis *et al.* 1995). In these models, patterns of enculturation and social interaction produce forces that affect the frequency of different culturally transmitted variants. For example, culturally transmitted variation between groups could lead to processes that favour cultural variants that enhance group success. The authors also argue that these models are consistent with the origin of human capacity for culture via ordinary Darwinian processes (Boyd and Richerson 1982).

David Sloan Wilson, an American evolutionary biologist, is a prominent proponent of group selection in evolution in general. Together with his compatriot Elliot Sober, a philosopher of biology, he proposed a framework of group selection called multilevel selection theory, which incorporates the approaches of gene-level selection and individual selection (Sober and Wilson 1998). Regarding cultural evolution in particular, he has made an interesting suggestion concerning evolution of religion (Wilson 2002). According to this suggestion, religion is a multilevel adaptation produced by cultural evolution through a multilevel selection process which has led to more cooperative and cohesive groups.

Group selection in general is not highly favoured among evolutionary biologists, the majority of whom most probably believe that, whenever possible, an explanation of biological evolution based on individual selection must be adopted owing to the principle of parsimony. It must, however, be emphasized that, while other models of evolution of cooperation, such as the kin-selection model, assume genetic inheritance, the group-selection models presuppose at least partial social transmission, via learning and teaching, of cultural traits. Therefore, the critical arguments against group selection in biological evolution do not apply to group selection in cultural evolution.

Many human cultural traits are most likely spandrels

Originally, 'spandrel' was an architectural concept referring to a three-sided space between two arches or between an arch and a rectangular enclosure, often decorated with paintings. In biology, spandrel refers to a phenotypic character that is a byproduct of evolution of some other character without itself being a result of the adaptive selection. Many human cultural characteristics are most obviously spandrels. For example, the skill of dancing most likely seems to be a byproduct of the ability to walk, and the capability to read and write almost certainly is a by product of speech. The spandrel concept in biology refers to the architectural analogy of evolution, presented in 1979 by the Harvard paleontologist Stephen Jay Gould and population geneticist Richard Lewontin (Gould and Lewontin 1979). In their paper, Gould and Lewontin employed the analogy of spandrels in Renaissance architecture: curved areas of masonry between arches supporting a dome that arise as a consequence of decisions about the shape of the arches and the base of the dome, rather than being designed for the artistic purposes for which they were often employed. The analogy emphasizes that organisms evolve as wholes rather than as collections of their characteristics. The authors criticize the idea of adaptationism, a theory that claims that all the characteristics of an organism are separate adaptations for some given function or 'purpose'.

Storage and accumulation of information in evolution of culture

The roots of human culture can be found in the early history of our species. As is well known, signs of culture, such as work and learning through teaching, are apparent among the great apes. However, it has not been observed that the great apes have, for instance, any division of labour or specialization in certain tasks, or any cooperation based on this, properties that belong to the most essential features of human culture. Nor have such features of development of human culture as a collection of cultural information and its storage in stocks outside the brain been observed in the great apes. Such stocks in modern human society are, for example, libraries and the Internet.

Further, as far as is known, no animal other than humans practises art and science in the usual sense of these words. Regarding the former, the oldest grooves and scrawls made on stone by anatomically modern humans, which can be interpreted as primitive art, are about 70,000 years old (Valladas *et al.* 2001). Ornaments made of clamshells have also been found that date back 90,000 years (Culotta 2010).

Science is a systematic enterprise that builds and organizes knowledge in the form of testable explanations and predictions about the universe. It is also a systematic and coherent body of universal and undisputed knowledge. It is commonly regarded that purposeful and systematic pursuit of such knowledge, in other words 'science', began in Mesopotamia about 10,000 years ago at the same time as mankind began cultivation of the soil, or agriculture. In fact, the word 'culture' (Latin, *cultura*) originally meant just agriculture. At that time, the first city states were also born, and division of labour became both possible and necessary. Could it be regarded that cumulative development of human culture started at that time?

Language as a necessary condition for evolution of culture

Language is a biological capacity that radically changed the chance for our species to succeed, and simultaneously occupy the entire planet. How language was born during our biological evolution is one of the most interesting questions of evolutionary biology. Understanding language evolution requires a theoretical framework explaining how Darwinian dynamics led to the many fundamental properties of human language. From the biological perspective, language is not a property of an individual, but the extended phenotype of a population. Consequently, the theory of evolution of language must be a population-level theory similar to evolutionary game theories (Nowak *et al.* 2002).

The American mathematical biologists Martin A. Nowak and Natalia L. Komarova have shown that biological and cultural evolution of language have proceeded hand in hand (Nowak and Komarova 2001). In another context, they, together with another writer, have discussed how formal language theory and learning theory can be extended to study language as a biological phenomenon, as a product of evolution (Nowak *et al.* 2002). They assumed that there is a population of individuals, and each individual uses a particular language. When individuals talk to each other, successful communication results in a payoff that contributes to biological fitness.

It has also been observed that in primates the species-specific size of the social group (Finlay and Darlington 1995) and the size of the brain (Dunbar 1992) are dependent on each other. The bigger the group size is, the larger are the brains of individual members of the group. This fact warrants the conclusion that evolution of the human brain and language has not been guided solely by ecological factors, but also by size of the social group and tight family relations. Accordingly, the newest theory hypothesizes that group size, size of the brain, intense family relations, and ability to speak have evolved side by side, these four factors reciprocally having an influence on one another's positive evolution (Durbar and Shultz 2007).

The central question concerning origin of human language is which genetic modifications led to the changes in brain structure that were decisive for it. Given the enormous complexity of this trait, several incremental steps guided by natural selection should be expected. In this process, evolution most likely reused cognitive features that evolved long ago and for other purposes (Nowak *et al.* 2002).

For the time being, the only gene known that has an effect on capacity to speak is the gene named *FOXP2* (forkhead box P2), discovered more than a decade ago. It was found in a Dutch family, some members of which suffered from a certain speech and language disorder, whereas in other sectors of psychological tests they performed normally (Fisher *et al.* 1998; Lai *et al.* 2001).

The protein produced by the *FOXP2* gene is a transcription factor guiding the function of a complete network of other genes. The network, in turn, regulates formation and function of muscles of the larynx. In addition, *FOXP2* is also important in the brain. The same gene, though in a different form, is found in the genomes of all mammals (Enard *et al.* 2002).

Evolution of the *FOXP2* gene in the human lineage appears to have been very rapid, and the human-specific form emerged around the same time that the human capacity for speech is believed to have developed (Enard *et al.* 2002; Zhang *et al.* 2002).

The gene network in the human brain regulated by the FOXP2 transcription factor has been analysed, and the ways in which it differs from the corresponding network in the brain of the chimpanzee have also been studied. Further, research has focussed on the regions of the brain in which the function of the target genes in the human brain is intensified or reduced in comparison with the brain of the chimpanzee (Spiteri *et al.* 2007; Konopka *et al.* 2009). The expression of the *FOXP2* gene in the cortex of the brain during fetal life is region-specific and most intense in the areas believed to be responsible for higher cognitive processes, such as thinking and language (Dominguez and Rakic 2009). In addition, many of the target genes regulated by FOXP2, which are expressed differently in man and chimpanzee, have been objects of positive selection in the human lineage (Konopka *et al.* 2009).

Prime differences between biological and cultural evolution

There are clear differences between biological and cultural evolution. Biological evolution is slow, whereas cultural evolution is rapid and accelerating. With regard to origin of new forms, cultural evolution is even more fruitful than biological evolution, especially when it comes to creative action and brilliance of individuals (Simonton 2000). The idea that biological evolution is preserving and conservative is also very firmly established; gene frequencies of populations usually remain the same, assuming that the ecological conditions do not change. Cultural evolution, in contrast, is cumulative, because it is based on the creative action of people, and because it involves collection and storage of information. As recently emphasized by Castro and Toro (2014), teaching as an accumulative mechanism of cultural inheritance, in its essence most likely absent in nonhuman primates, has played a significant role in our cumulative cultural evolution. As cultural traits become more complex, cumulative cultural transmission requires incremental teaching to ensure accurate transmission from one generation to the next.

The idea that biological evolution is not directed, whereas cultural evolution at least can be oriented (and, at its best, conceived), is also widely accepted. It is also known that biological evolution is irreversible and nonrepetitive. Simply put, natural selection cannot run in counter flow, and, for example, an extinct species never returns. In contrast, however, cultural evolution can, as is well known, be partly reversible and repetitive, as many examples in the history of mankind—for instance, the Renaissance—illustrate.

Further, it is well known that biological evolution is purposeless and opportunistic as well as without direction.

Evolution of culture, however, is purposeful because it depends on the intentions of human individuals and societies. Consequently, it follows that cultural evolution in principle is goal-oriented. Both biological and cultural evolution create order, each in its own realm. In other words, they resist growth of entropy. This can happen because both are open systems. However, the resistance to growth of entropy occurs in different ways in these two forms of evolution. The openness of the biosphere of the earth rests on the energy from the Sun or some other source, such as the energy derived from hot springs located at the bottom of the oceans. The evolution of culture, in contrast, receives its energy from the labour of human beings, and rests on the collection and storage of information in human brains or stocks outside these brains.

Biological evolution and cultural evolution affect each other

Evolution of human culture has proceeded hand in hand with biological evolution of our species; in other words, our biology and culture have experienced coevolution. These two forms of evolution have many similarities, but also show clear differences, as shown earlier in this paper.

Perhaps the most important of the similarities is the principle of selection. It seems that selection (though not only natural selection) is possibly the sole mechanism in both biological and cultural evolution that creates information and increases its quantity. Selection causes an increase in the amount of negative entropy or enthalpy. The general theory of selection seems to be valid in both biological evolution and, at least to a certain degree, evolution of culture.

In his monumental work *The Structure of Evolutionary Theory*, Stephen J. Gould emphatically presents the view that in biological evolution selection occurs at several levels, beginning at the level of genes and passing through the level of individuals and ending at the level of populations and species (Gould 2002 pages 595–744). Without doubt, this form of hierarchical model of selection applies even better to evolution of culture than to evolution of the biosphere. Within the realm of culture, selection, which, in contrast to biological evolution is in this case at least partly conscious, consists of decisions made by individuals, teams, different societies and institutions, and finally by entire societies and all of mankind.

Culture modifies our genome

Through its own activity, the human species modifies its ecological niche, for example by cultivating the soil, raising livestock and building dwellings. Many specific examples can be pointed to, indicating that numerous interactions of culture and the genome have influenced biological evolution of mankind. Reciprocally, biological evolution has had an effect on evolution of culture. Modern studies dealing with genetic variation in humans have revealed that hundreds of genes have been targets of positive selection during recent human evolution. Moreover, this has occurred as a response to mankind's own activity—in other words, culture (Laland *et al.* 2010). Evidently, therefore, coevolution of our genome and culture is still continuing.

Concrete examples can be presented concerning how changes in diet have modified our genome, and reciprocally how evolution of the genome has shaped our diet (Arjamaa and Vuorisalo 2010; Fisher and Ridley 2013). Of these, the most intensively studied is the connection between animal husbandry and adult lactose tolerance. In point of fact, lactose intolerance, often regarded as an illness, is not a disease at all, but an original human condition. Most people lose the ability to tolerate lactose after childhood, but in some populations activity of the lactase enzyme, which breaks down lactose, persists even in most adults. This trait is called lactose tolerance, and it occurs commonly in northern Europe, Russia, North America, among the nomads of Africa, and in the Middle East, but is rare or absent elsewhere. Populations in which lactose tolerance is common use cattle or camel milk or milk products as a nutriment.

Lactose tolerance among the Nordic people mentioned above is a consequence of a mutation in the regulatory part of the gene coding for the lactase enzyme. The mutation causes lactase to continue to be synthesized in the small intestine in adulthood. It has occurred independently twice: first in the Ural Mountains 12,000–5,000 years ago, and the second time in the Caucasus 3000–1400 years ago. The gene allele that emerged has then, owing to natural selection, become more and more common in those populations in which cattle milk has been used as nutriment (Enattah *et al.* 2007). Another mutant form of the gene encoding lactase and producing lactose tolerance was born in Saudi Arabia about 6000 years ago in association with the use of camel milk (Arjamaa and Vuorisalo 2010).

A second example relating to association of diet with biological evolution involves consumption of starch and the gene responsible for its digestion. Food containing significant quantities of starch is consumed by people practising agriculture, as well as hunter-gatherers in arid areas. Other hunter-gatherers and nomadic peoples consume only small amounts of starch. Consumption of starch seems to be associated with the number of copies of the gene for the amylase enzyme in the genome. People who consume large quantities of starch have, on average, more copies of this gene in their genomes than do those that consume less starch (Laland *et al.* 2010).

The foregoing examples are clear cases of genomic changes that are consequences of cultural innovations. Such examples are mostly drawn from the time after the Neolithic revolution and the invention of agriculture (Fisher and Ridley 2013). It has, however, also been suggested by the British primatologist Richard Wrangham that invention of fire and cooking had already altered human gut size two million years ago, positing that genetic change was contingent on prior cultural invention (Wrangham 2009). Thus, culture-driven gene evolution may have operated very early in evolutionary history of our species, and may even be key to understanding our origin. In addition to Wrangham's argument, ideas on evolution of spoken language support this notion. Genomic alterations that facilitated spoken language, such as the human form of the *FOXP2* gene dealt with earlier, might have spread through our ancestors after this trait emerged (Fisher and Ridley 2013). According to Lai *et al.* (2001), changes in the human FOXP2 protein predated the splitting of Neanderthals and modern humans several hundred thousand years ago. Most recently, intronic noncoding changes have been pinpointed to the *FOXP2* locus that developed after the split from Neanderthals and that might have affected regulation of functioning of the gene (Maricic *et al.* 2013).

Characteristics pointing at the coevolution of genes and culture have also been observed among such clearly cultural traits as learning, teaching, and the social transfer of culture. Such characteristics seem to be intelligence, certain features of behaviour and personality, as well as the talent for cooperation (Laland *et al.* 2010).

These kinds of studies, mostly based on molecular genetics, have indicated that the dynamics of coevolution of the genome and culture are stronger, more rapid and more extensive than the dynamics of biological evolution. This fact has led some researchers in the field to conclude that coevolution of the genome and culture is the most important form of human evolution (Laland *et al.* 2010). In this context, attention should be called to behavioural epigenetics, a new study area examining the role of epigenetics in shaping the behaviour of animals and humans as a potential factor in evolution of culture—a topic that so far has been little studied (Miller 2010).

Coevolution of genes and culture is still continuing

Modern methods of molecular genetics have made it possible to study in detail consequences of selection on the genome of any species. The evolutionary history of a species is, so to speak, written in its DNA sequence. It is very likely that modification of its own ecological niche by means of culture has strongly influenced, and continues to influence, genetic evolution of mankind (Laland *et al.* 2010). Estimates of the number and proportion of genes that have been undergoing rapid evolution during the last 50,000 years vary from a few hundred to two thousand. It has been estimated that a total of ten per cent of the human genome may have been linked to genes that have been targets of positive selection (Williamson *et al.* 2007).

Even though in most cases it is not yet possible to specify precisely which phenotypic characteristics selection has targeted, or what the circumstances were that favoured these phenotypes, conventions coupled to culture are strong candidates for selective factors. Geneticists are increasingly inclined to consider culture to be an important selective factor in biological evolution of man (Hawks *et al.* 2007; Varki *et al.* 2008). Naturally, biological evolution still operates on the basis of how capable individuals produce fertile offspring, but culture has brought with it a new factor that causes differences in biological fitness. It is often unclear, however, how the different aspects of culture affect fitness, and which component in each case is being targeted by the effect. Nevertheless, it can be said, for instance, that development of medicine and hygiene, in addition to improvement of mankind's nutritional situation, have had an effect on all three components of fitness.

Researchers of coevolution of genes and culture consider culture to be a dynamic occurrence capable of modifying the material world. Models they have developed have demonstrated that culture can have a strong influence on the rate of evolution of gene frequencies in human populations, sometimes accelerating it, sometimes slowing it. Recent estimates of the magnitude of selection caused by culture suggest a very strong selection (Laland *et al.* 2010, and references therein).

The scientific results referred to above challenge the central presupposition of evolutionary psychology, according to which human behavioural characteristics were, for the most part, determined in the evolutionary environment that prevailed during the Palaeolithic Stone Age hundreds of thousands of years ago. On the contrary, it seems today that human behavioural traits are flexible and constantly under the influence of culture. In addition, evolutionary psychology assumes that behind all human cultural variation is a rather rigid universal human nature that evolved via biological evolution during the Pleistocene, when humans were hunter-gatherers (Crawford 1998). However, if a universal human nature exists at all, it has become flexible through biological evolution, and is thus open to changes caused by learning and other events coupled with development (Wheeler and Clark 2008).

The incorporation of biology and culture

Using the language analogy of theoretical biology first presented by the Scottish developmental biologist Conrad H. Waddington in 1972 (Waddington 1972), the American epidemiologist Rodrick Wallace and his compatriot, phylogeographer Robert G. Wallace (Wallace and Wallace 1999), have proposed that the joint evolution of human biology and culture rests on the merging together of the genetic 'language' and the cultural 'language', language being understood in the broadest sense of the word. Subsequent to this incorporation, it became possible for human societies to be homes for specializations and assimilations that are characteristic only of culture.

In this way, morality, religions, art, science, political and economic systems, and the entirety of human culture in all its richness have emerged.

Acknowledgements

I thank my friend Senior Lecturer Timo Vuorisalo, Ph.D., Department of Biology, University of Turku, for critical reading of the first version of the manuscript and many suggestions for improvement. Special thanks are given to Maaria Tringham, M.Sc., and Damon Tringham, M.Phil., for checking the language, as well as amanuensis Matti Ketola, Department of Biology, University of Turku, for drawing the figure.

References

Aldrich H. E., Hodgson G. M., Hull D. L., Knudsen T., Mokyr J. and Vanberg V. J. 2008 In defence of generalized Darwinism. *J. Evol. Econ.* **18**, 577–596.

Alexander R. D. 1987 *The Biology of moral systems*. Aldine De Gruyter, New York, USA.

Allen B., Nowak M. A. and Wilson E. O. 2013 Limitations of inclusive fitness. *Proc. Natl. Acad. Sci. USA* **110**, 20135–20139.

Arjamaa O. and Vuorisalo T. 2010 Gene-culture coevolution and human diet. *Am. Sci.* **98**, 140–147.

Boyd R. and Richerson P. J. 1981 Culture, biology and the evolution of variation between human groups. In *Science and the question of human equality* (ed. M. S. Collins, I. W. Wainer and T. A. Bremmer). pp. 99–152. Westview Press, Boulder, Colorado.

Boyd R. and Richerson P. J. 1982 Cultural transmission and the evolution of cooperative behavior. *Hum. Ecol.* **10**, 325–351.

Boyd R. and Richerson P. J. 1985 *Culture and the evolutionary process*. University of Chicago Press, Chicago, USA.

Boyd R. and Richerson P. J. 1989 The evolution of indirect reciprocity. *Soc. Networks* **11**, 213–236.

Castro L. and Toro M. A. 2014 Cumulative cultural evolution: the role of teaching. *J. Theor. Biol.* **347**, 74–83.

Cavallaro S., D'Agata V., Manickam P., Dufour F. and Alkon D. L. 2002 Memory-specific temporal profiles of gene expression in the hippocampus. *Proc. Natl. Acad. Sci. USA* **99**, 16279–16284.

Cavalli-Sforza L. L. and Feldman M. W. 1981 *Cultural transmission and evolution: a quantitative approach*. Princeton University Press, Princeton, USA.

Crawford C. 1998. Environments and adaptations: then and now. In *Handbook of evolutionary psychology: ideas, issues, and application.* (ed. C. Crawford and D. L. Krebs). pp. 275–302, Lawrence Erlbaum, Mahwah, USA.

Culotta E. 2010 Did modern humans get smart or just get together? *Science* **328**, 164.

Darwin C. 1913 *The Descent of man and selection in relation to sex.* A reprint of the second edition. John Murray, London.

Darwin C. 1968 *The origin of species by means of natural selection or the preservation of favoured races in the struggle for life.* A reprint of the sixth edition. Oxford University Press, London.

Davidson J. E. and Sternberg R. J. 2003 *The psychology of problem solving*. Cambridge University Press, Cambridge, UK.

Dawkins R. 1982 *The extended phenotype: the gene as the unit of selection*. Freeman, San Francisco.

Dawkins R. 2006 *The selfish gene.* 30th Anniversary edition. Oxford University Press, Oxford.

Deevey E. S. 1960 The human population. *Sci. Am.* **203**, 194–204.

Dominguez M. H. and Rakic P. 2009 The importance of being human. *Nature* **462**, 169–170.

Dunbar R. I. M. 1992 Neocortex size as a constraint on group size in primates. *J. Hum. Evol.* **22**, 469–493.

Durbar R. I. M. and Shultz S. 2007 Evolution in the social brain. *Science* **317**, 1344–1347.

Durham W. H. 1982 Interactions of genetic and cultural evolution: models and examples. *Hum. Ecol.* **10**, 289–323.

Enard W., Przeworski M., Fisher S. E., Lai C. S. L., Wiebe V., Kitano T. *et al.* 2002 Molecular evolution of FOXP2, a gene involved in speech and language. *Nature* **418**, 869–872.

Enattah N. S., Trudeau A., Pimenoff V., Maiuri L., Auricchio S., Greco L. *et al.* 2007 Evidence of still-ongoing convergence evolution of the lactase persistence T_{-13910} alleles in humans. *Am. J. Hum. Genet.* **81**, 615–625.

Ewens W. J. 1969a Mean fitness increases when fitnesses are additive. *Nature* **221**, 1076.

Ewens W. J. 1969b A generalized theorem of natural selection. *Genetics* **63**, 531–537.

Ewens W. J. 1989 An interpretation and proof of the fundamental theorem of natural Selection. *Theor. Popul. Biol.* **36**, 167–180.

Ewens W. J. 1992 An optimizing principle of natural selection in evolutionary population genetics. *Theor. Popul. Biol.* **42**, 333–346.

Feldman M. W. and Laland K. N. 1996 Gene-culture coevolutionary theory. *Trends Ecol. Evol.* **11**, 453–457.

Finlay B. L. and Darlington R. B. 1995 Linked regularities in the development and evolution of mammalian brains. *Science* **268**, 1578–1584.

Fisher R. A. 1958 *The genetical theory of natural selection.* Second revised edition. Dover Publications, New York, USA.

Fisher S. E. and Ridley M. 2013 Culture, genes, and the human revolution. *Science* **340**, 929–930.

Fisher S. E., Vargha-Khadem F., Watkins K. E., Monaco A. P. and Pembrey M. E. 1998 Localisation of a gene implicated in a severe speech and language disorder. *Nat. Genet.* **18**, 168–170.

Fletcher J. A. and Zwick M. 2006 Unifying the theories of inclusive fitness and reciprocal altruism. *Am. Nat.* **168**, 252–262.

Frank S. A. 1997 The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis. *Evolution* **51**, 1712–1729.

Gould S. J. 2002 *The structure of evolutionary theory*. The Belknap Press of Harvard University Press, Cambridge (Ma) and London.

Gould S. J. and Lewontin R. C. 1979 The spandrels of San Marco and the panglossian paradigm: A critique of the adaptationist programme. *P. Roy. Soc. London. Ser. B.* **205**, 581–598.

Hamilton W. D. 1963 The evolution of altruistic behavior. *Am. Nat.* **97**, 354–356.

Hamilton W. D. 1964 The genetical evolution of social behavior. I, II. *J. Theor. Biol.* **7**, 1–16, 17–52.

Hawks J., Wang E. T., Cochran G. M., Harpending H. C. and Moyzis R.K. 2007 Recent acceleration of human adaptive evolution. *Proc. Natl. Acad. Sci. USA* **104**, 20753–20758.

Heyes C. M. and Frith C. D. 2014 The cultural evolution of mind reading. *Science* **344**, 124391.

Hilbe C., Traulsen A., Röhl T. and Milinski M. 2014 Democratic decisions establish stable authorities that overcome the paradox of second-order punishment. *Proc. Natl. Acad. Sci. USA* **111**, 752–756.

Hoebel E. A. 1972 *Anthropology: study of man*. McGraw Hill, New York, USA.

Hull D. L. 1988 *Science as a process: an evolutionary account of the social and conceptual development of science*. University of Chicago Press, Chicago, USA.

Hull D. L. 2001a *Science and selection: essays on biological evolution and the philosophy of science*. Cambridge University Press, Cambridge, UK.

Hull D. L. 2001b The success of science and social norms. *Hist. Phil. Life Sci.* **23**, 341–360.

Hull D. L., Langman R. and Glenn S. 2001 A general account of selection: biology, immunology and behavior. *Behav. Brain Sci.* **24**, 511–528.

Konopka G., Bomar J. M., Winden K., Coppola G., Jonsson Z. O., Gao F. *et al.* 2009 Human-specific transcriptional regulation of CNS development genes by FOXP2. *Nature* **462**, 213–218.

Korotayev A. 2004 *World religions and social evolution of the old world oikumene civilizations: a cross-cultural perspective*. Edwin Mellen Press, New York, USA.

Lai C. S. L., Fisher S. E., Hurst J. A., Vargha-Khadem F. and Monaco A. P. 2001 A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature* **413**, 519–523.

Laland K. N., Odling-Smee J. and Myles S. 2010 How culture shaped the human genome: bringing genetics and the human sciences together. *Nat. Rev. Genet.* **11**, 137–148.

Lewontin R. 1970 The units of selection. *Annu Rev. Ecol. Syst.* **1**, 1–18.

Lewontin R. 1982 *Human diversity*. Scientific American Books, New York, USA.

Lewontin R. 2000 *The triple helix: gene, organism and evolution*. Harvard University Press, Cambridge, USA.

Maricic T., Günther V., Georgiev O., Gehre S., Ćurlin M., Schreiweis C. *et al.* 2013 A Recent Evolutionary Change Affects a Regulatory Element in the Human FOXP2 Gene. *Mol. Biol. Evol.* **30**, 844–852.

Mesoudi A. and Whiten A. 2008 The multiple roles of cultural transmission experiments in understanding human cultural evolution. *Philos. Trans. R. Soc. London, Ser. B* **363**, 3489–3501.

Miller G. 2010 The seductive allure of behavioral epigenetics. *Science* **329**, 24–27.

Nesse R. M. 2009 Social selection and the origins of culture. In *Evolution, culture and the human mind*. (ed. M. Schailer, S. J. Heine, A. Norenzayan, T. Yamagishi and T. Kameda). pp. 137–150. Lawrence Erlbaum Associates, Philadelphia, USA.

Nettle D. 2009 Ecological influences on human behavioural diversity: a review of recent findings. *Trends Ecol. Evol.* **24**, 618–624.

Nowak M. A. and Komarova N. L. 2001 Towards an evolutionary theory of language. *Trends Cogn. Sci.* **5**, 288–295.

Nowak M. A., Komarova N. L. and Niyogi P. 2002 Computational and evolutionary aspects of language. *Nature* **417**, 611–617.

Pagel M. 2009 Human language as a culturally transmitted replicator. *Nat. Rev. Genet.* **10**, 405–415.

Pigliucci M. 2007 Do we need an extended evolutionary synthesis? *Evolution* **61**, 2743–2749.

Portin P. 2012 Does epigenetic inheritance revolutionize the foundations of the theory of evolution? *Curr. T. Genet.* **5**, 49–59.

Price G. R. 1970 Selection and covariance. *Nature* **227**, 520–521.

Price G. R. 1972a Extension of covariance selection mathematics. *Ann. Hum. Genet.* **35**, 485–490.

Price G. R. 1972b Fisher's 'fundamental theorem' made clear. *Ann. Hum. Genet.* **36**, 129–140.

Queller D. C. 1992 A general model for kin selection. *Evolution* **46**, 376–380.

Rampon C., Jiang C. H., Dong H., Tang Y-P., Lockhart D. J., Schultz P. G. *et al.* 2000 Effects of environmental enrichment on gene expression in the brain. *Proc. Natl. Acad. Sci. USA* **97**, 12880–12884.

Richards R. J. 1977 The natural selection model of conceptual evolution. *Philos. Sci.* **44**, 494–501.

Richards R. J. 1987 *Darwin and the emergence of evolutionary theories of mind and behavior*. University of Chicago Press, Chicago, USA.

Russell C. and Russell W. M. S. 1989 Cultural evolution of behaviour. *Neth. J. Zool.* **40**, 745–762.

Simon B. 2014 Continuous-time models of group selection, and the dynamical insufficiency of kin selection models. *J. Theor. Biol.* **349**, 22–31.

Simonton D. K. 2000 Human creativity, cultural evolution and niche construction. *Behav. Brain Sci.* **23**, 159–160.

Sober E. and Wilson D. S. 1998 *Unto ioothers: the evolution and psychology of unselfish behavior*. Harvard University Press, Cambridge, USA.

Soltis J., Boyd R. and Richerson P. J. 1995 Can group-functional behaviors evolve by cultural group selection? *Curr. Anthropol.* **36**, 473–494.

Spiteri E., Konopka G., Coppola G., Bomar J., Oldham M., Ou J. *et al.* 2007 Identification of the transcriptional targets of FOXP2, a gene linked to speech and language, in developing human brain. *Am. J. Hum. Genet.* **81**, 1144–1157.

Stephens C. 1996 Modeling Reciprocal Altruism. *Brit. J. Philos. Sci.* **47**, 533–551.

Strimling P., Enquist M. and Eriksson K. 2009 Repeated learning makes cultural evolution unique. *Proc. Natl. Acad. Sci. USA* **106**, 13870–13874.

Trivers R. L. 1971 The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57.

Valladas H., Clottes J., Genese J., Garcia M. A., Arnold M., Cachier H. *et al.* 2001 Palaeolithic paintings – evolution of prehistoric cave art. *Nature* **413**, 479.

Varki A., Geshwind D. H. and Eichler E. E. 2008 Explaining human uniqueness: genome interactions with environment, behavior and culture. *Nat. Rev. Genet.* **9**, 749–763.

Waddington C. H. 1972 *Towards a theoretical biology.* Vol. 4. Essays. Edinburgh University Press, Edinburgh, Scotland.

Wallace R. and Wallace R. G. 1999 Organisms, organizations and interactions: an information theory approach to biocultural evolution. *BioSystems* **51**, 101–119.

Wang Z., Szolnoki A. and Perc M. 2014 Rewarding evolutionary fitness with links between population promotes cooperation. *J. Theor. Biol.* **349**, 50–56.

Weismann A. 1892 *Das Keimplasma. Eine Theorie der Vererbung*. Gustav Fischer, Jena.

Weismann A. 1893 *Über die Vererbung*. Gustav Fischer, Jena.

West-Eberhard M. J. 1979 Sexual selection, social competition and evolution. *Proc. Am. Phil. Soc.* **123**, 222–234.

West-Eberhard M. J. 1983 Sexual selection, social competition and speciation. *Q. Rev. Biol.* **58**, 155–183.

Wheeler M. and Clark A. 2008 Culture, embodiment and genes: unravelling the triple helix. *Philos. Trans. R. Soc. London, Ser. B* **363**, 3563–3575.

Williamson S. H., Hubisz M. J., Clark A. G., Payseur B. A., Bustamante C. D. and Nielsen R. 2007 Localizing recent adaptive evolution in the human genome. *PLoS Genet.* **3**, e90.

Wilson D. S. 2002 *Darwin's Cathedral: Evolution, Religion, and the Nature of Society*. University of Chicago Press, Chicago, USA.

Wrangham R. 2009 *Catching fire: how cooking made us human*. Basic Books, New York, USA.

Zhang J., Webb D. M. and Podlaha O. 2002 Accelerated protein evolution and origins of human-specific features: Foxp2 as an example. *Genetics* **162**, 1825–1835.

Zhang M. and Gong T. 2013 Principles of parametric estimation in modeling language competition. *Proc. Natl. Acad. Sci. USA* **110**, 9698–9703.

Received 17 April 2014, in revised form 1 August 2014; accepted 18 August 2014
Unedited version published online: 21 August 2014
Final version published online: 24 February 2015