Other buildings comprising the Institute are the Jacques Loeb Laboratories in the Marine Biological Laboratory at Woods Hole, Mass., for those wishing to study marine organisms. Special facilities are also available in the research laboratories of the New York Botanical Garden for those members of the faculty who desire to use the extensive resources there.

Because of increasing dependence of modern scientific research on adequate technical facilities, many supporting services are maintained in order to facilitate and make more effective the work of the Institute. For example, the Animal House contains 40,000 sq. ft. of quarters for animals ranging in size from mice to horses. There are well-equipped shops for the construction of instruments and electronic equipment; whereas shops for machine work and cabinet work make possible the construction and maintenance of all laboratory equipment. Central facilities for electron microscopy, spectroscopic determinations, microanalyses, X-ray studies, photographic work and media preparation are among the many aids maintained for the general use of the various laboratories.

Publications

The Rockefeller Institute Press was established in 1958 and now publishes *The Journal of Experimental Medicine*, *The Journal of General Physiology* and *The Journal of Biophysical and Biochemical Cytology*. Reprints of recent publications are issued periodically as volumes of *Studies*. Events of general interest are published in *The Rockefeller Institute Quarterly*. Monographs and scientific texts are to be published by the Rockefeller Institute Press in association with Oxford University Press.

The celebrations of the first Convocation of the Rockefeller Institute were rounded off by a pleasant garden party in the grounds of the President's House.

In announcing his resignation from the presidency of the Board of Trustees of the Rockefeller Institute in 1950, Mr. John D. Rockefeller, jun., said he had always regarded "this enterprise as the most significant and the most permanent of any that my father established". It is certainly true that the world of scholarship, and especially of science and medicine, owes a great debt of gratitude to the Rockefeller family: particularly through the Rockefeller Institute is the world indebted to John D. Rockefeller, his son John D. Rockefeller, jun., and his son David Rockefeller.

To Dr. Detlev Bronk the world of science and learning will tender their congratulations and express deep admiration for his almost superhuman efforts to further the development and advancement of the Rockefeller Institute and especially for the foundation of this new graduate university.

EVOLUTIONARY SYSTEMS—ANIMAL AND HUMAN*

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THE major advance in the theory of biological evolution since Darwin's day has been the rise of Mendelian genetics. It is scarcely an exaggeration to say that when Darwin wrote biology possessed no theory of inheritance. Since then, the existence of more or less discrete hereditary factors has been discovered, their position in the cell ascertained to be on the chromosomes in the nucleus, and the behaviour of these chromosomes analysed in great detail both in normal and in various more or less unusual conditions.

The whole of this complex of phenomena which are concerned with the manner in which hereditary determinants are passed on from one generation to the next may be referred to as the 'genetic system'. From the point of view of evolutionary theory three main points have emerged concerning it. The first is that the existence of discrete hereditary determinants safeguards variation against being lost if dissimilar animals cross-breed, as Darwin feared it might[1]. Indeed the fact that during the greater part of the life-cycle of most animals and plants the hereditary factors are present in the diploid condition implies that most organisms carry within them much greater potentialities for variation in their offspring than would appear at first sight. The second point, which is one that we owe primarily to the insight of Darlington[2], is that the genetic system itself can be regarded not only as an agent but also as a subject of evolutionary change, which is to say that the genetic system itself evolves. This I shall return to later.

The third point concerns the origin of new variation. It is essential to any theory of evolution that there must be some mechanism by which new variation is brought into being. Darwin was driven to speculate as to what this mechanism might be. In the absence of any understanding of how hereditary qualities are transmitted, he made no pretence that he had found a solution fully satisfactory to himself, although he was somewhat tempted by the theory, usually associated with the name of Lamarck, that characters acquired by organisms in the course of their lifetime might be transmitted to their offspring. Later experimental investigations have shown that in general this is not so.

Our knowledge of the genetic system, which is very extensive and detailed, forces us to the conclusion that the origin of new hereditary variation is to be found only in alterations and rearrangements of the atomic groupings out of which the hereditary factors of the chromosomes are composed. These alterations follow rules of stability which are still entirely unknown to us, but which must be properties of the hereditary molecules themselves and have little or no relation to the precipitating events by which the alterations were stimulated. One of the most firmly based doctrines of modern genetics is that mutation is a random process. I do not wish to challenge this, but I shall suggest later that some care is necessary in interpreting the word random.

* Substance of the Woodhull Lecture delivered at the Royal Institution on February 27.

In present-day biology, evolution is envisaged as resulting from the interaction between, on one hand, the genetic system characterized by random mutation, and on the other, natural selection. The evolutionary pressures exerted by these two factors are exhibited as being quite external to the nature of the organisms involved. The essential evolutionary pressure exerted by the genetic system is that of mutation, and mutation, it is explained, is a random process. Any explanation which might be offered for the nature of the mutational changes would have to be found, it is asserted, in the chemical composition of the genes and not in the nature of the complete biological organism in which these genes are carried. Mutation thus appears as essentially an external force to which the organism passively submits. Again, natural selective pressures are usually thought of as arising simply from the external environment. When the climate changes, a new predator appears, or industrial fumes blacken the tree trunks on which the animal lives, the populations of organisms concerned cannot, it is usually implied, do anything but submit to these pressures and wait until the equally uncontrollable process of mutation throws up a new hereditary variant which enables them to meet the environment's challenge more successfully.

The time seems to have come when we need to take into account two further aspects of the evolutionary mechanism[3]. In the first place, natural selective pressures impinge not on the hereditary factors themselves, but on the organisms as they develop from fertilized eggs to reproductive adults. We need to bring into the picture not only the genetic system by which hereditary information is passed on from one generation to the next, but also the 'epigenetic system' by which the information contained in the fertilized egg is expanded into the functioning structure of the reproducing individual. Each organism during its lifetime will respond in some manner to the environmental stresses to which it is submitted, and in a population there is almost certain to be some genetic variation in the intensity and character of these responses. Natural selection will favour those individuals in which the responses are of most adaptive value.

Two consequences can be expected to follow, and have in fact been demonstrated experimentally. In the first place, natural selection will build up genotypes which set going developmental mechanisms which easily respond to environmental stresses by the production of a well-organized modification which is of adaptive value. It will, as it were, build into the genotype a gun which is not only set on a hair trigger but which is aimed to hit the target when it goes off. In so far as such a developmental response becomes precisely delimited and easily initiated, it becomes the more likely to be produced by unspecified changes in the chemical nature of the hereditary substance. Mutations, which we can think of as random when we are considering the nucleo-proteins of the chromosomes, will have effects on the phenotype of the organisms which are not necessarily random, but which will be modified by the types of instability which have been built into the epigenetic mechanisms by selection for response to environmental stresses.

Since this is an unfamiliar point of view it may be as well to illustrate it by actual example[4]. If eggs of *Drosophila* are submitted to ether vapour shortly after laying, a proportion of them tend to have their development modified so that they produce a very peculiar phenotype, known as bithorax, in which the third segment of the thorax of the animal is transformed from its normal small and obscure structure into a duplicate of the large second thoracic segment. We can treat the response as though it were favoured by selection, and in each generation breed from those individuals in the population which respond to the stress in this way. When this was done with a population taken from a normal wild-type stock, it became apparent that there was some genetic variation of the capacity to respond in this manner. If selection favoured the response, the frequency with which it occurred increased from generation to generation, until after some time it became practically universal when the selected stock was submitted to the ether. After some time a new gene mutation occurred; this was a sex-linked factor which had not been present in the original stock. Its effect is that females homozygous for it lay eggs which tend to develop the bithorax phenotype. This is particularly striking when the factor is present in the selected stock, in which, as it were, the bithorax modification has been set on a hair trigger. If the factor is transferred into an unselected wild-type stock, the tendency to produce bithoraxes is very much reduced. We have here an example in which selection has built up a genotype which exhibits a particular type of developmental instability. A gene mutation has occurred which in the normal *Drosophila* would have only a very slight tendency to produce this phenotype, but which does so with considerable frequency in the selected stock. Thus, if one merely refers to such a gene mutation as 'random', one does not say by any means everything of interest which can be told about it.

The other main evolutionary effect of the epigenetic system depends on the fact that the development of organisms is usually to some extent canalized, in the sense that even though it may become somewhat modified in response to an environmental stress, it also exhibits a tendency to reach its normal end-result in spite of disturbing circumstances If a strain of animals is selected over many generations for its capacity to respond in a particular way to a certain stress, a set of genotypes will be built up in which this response is easily exhibited when the environmental stress is applied, but the developmental resistance to change may be sufficient to ensure that some of it is still retained even if the stress is removed. If that happens, we should have a system which exactly mimics the inheritance of an acquired character, but one which depends not on the direct induction of a hereditary variation, in the manner suggested by Lamarck, but on selection operating on the genetical structure of the population.

Again, there is a practical chapter and verse for such a suggestion in the experiments with the bithorax modification. After rather more than 20 generations of selection for ease of response to ether vapour, the strain had reached a condition in which a high proportion of bithorax individuals appeared even when the ether treatment was not given. This is the process which I have spoken of as the 'genetic assimilation' of an acquired character.

To obtain a complete picture of the evolutionary system, we need to take into account one further set of factors. These may be spoken of as the exploitive system. Animals—the following considerations do not apply so directly to plants—are usually surrounded by a much wider range of environmental conditions than they are willing to inhabit. They live in a highly heterogeneous 'ambiance', from which

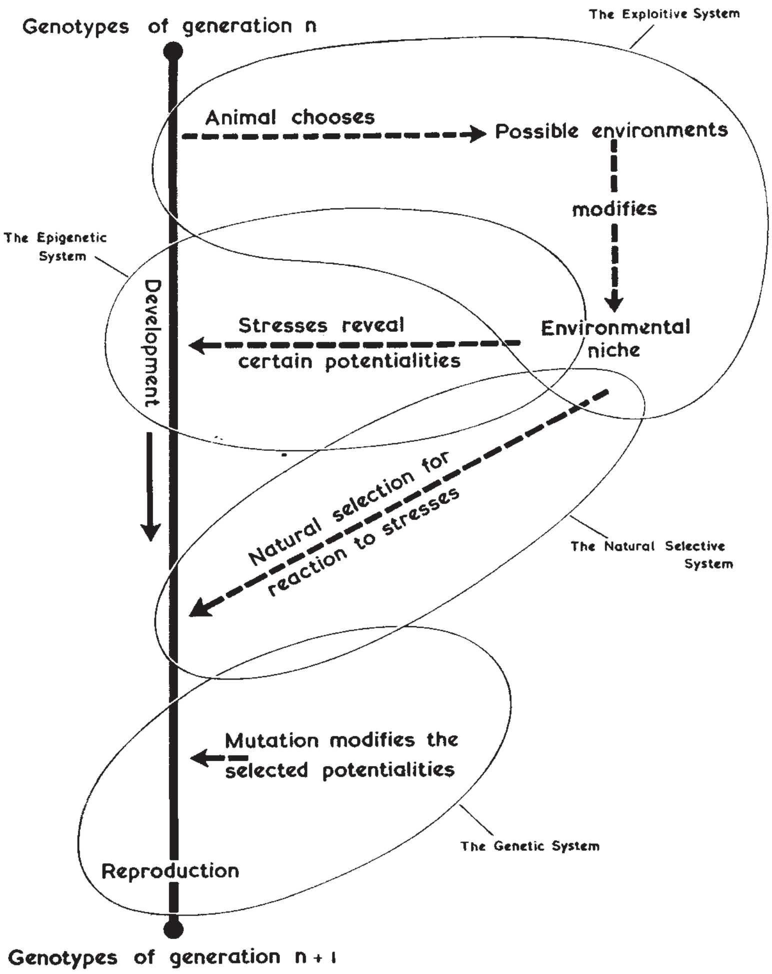

Fig. 1. The logical structure of the biological evolutionary system

mechanism. Indeed, it might be not unreasonable to define humanity by this fact. In man, the processes of teaching by the older members of the population, and learning by the younger ones, have been carried to an incomparably higher pitch than is found in any of the prehuman forms of life, where they play only a relatively minor part, for example, in the determination of bird song, and a few other examples. In man, they have developed not only to highly effective person-to-person learning, as in apprenticeship, but, by the invention of writing and other more recent devices, to an extremely elaborate system by which the whole conceptual understanding of the past is made available to present recruits to human society. We have here what in effect amounts to a new mode of hereditary transmission. It may be referred to as the cultural or 'socio-genetic' system.

Within the past few millennia, the human race has acquired capacities which, in the non-human world, could only have been obtained as the results of evolution. To give a banal example, one may mention the ability to fly. Man has certainly not achieved this capacity by waiting for genes to turn up which have transformed his forelimbs into wings. In fact there is no evidence that changes in the pool of genes available to the human race had any specific effect on the development of the human conquest of the air. This does not mean, of course, that the genes were

they themselves select the particular habitat in which their life will be passed. Thus the animal by its behaviour contributes in a most important way to determining the nature and intensity of the selective pressures which will be exerted on it. Natural selection is very far from being as external a force as the conventional picture might lead one at first sight to believe.

The problems which arise in this field have as yet been rather little studied, even in the biological field, where the relations are likely to be relatively simple. This area of study is, however, likely to be of particular importance for eugenics, since human behaviour is incomparably more elaborate than that of the majority of animals, and in particular the behaviour associated with choice and the seeking of particular goals is much more fully developed.

Biological evolution, then, is carried out by a mechanism which involves four major factors: a genetic system, an epigenetic system, an exploitive system, and a system of natural selective pressures (Fig. 1). All these factors undoubtedly persist in man, but, just as the genetic system is itself subject to evolution, so in broader terms we may say that this whole four-component evolutionary system, of which the genetic system is only a part, itself evolves. The human situation is characterized by an enormously important step in the evolution of the evolutionary

irrelevant. Human inventiveness and skill, just like any character of any organism, are produced by the interaction of genes with one another and with the environment during development. But so far as one can tell, all the genes necessary to produce men capable of inventing methods of flying had been present in the human population for many generations. What the development of flight was waiting for was not some change in the genetic system, but some change in the cultural system.

When one attempts to consider the problem of human evolution, the type of phenomena which should rise to one's mind are all the most crucial changes which have occurred between, say, the late Stone Age and the present. It is not in any important sense the slight changes in bodily structure which differentiate us from Cromagnon man which make the greatest impression. Human evolution has been in the first place a cultural evolution.

It is important not to overlook this first impression of what human evolution is all about. It is clear that for an understanding of how the human race has come into the possession of those characteristics which we now think most valuable in human life, a theory is needed which is primarily one of cultural evolution.

It seems probable that in the cultural evolutionary system there are parallels for many of the factors operative in the biological system. For example, parallel to the process of gene mutation there is the arising of new ideas capable of cultural transmission; and there are undoubtedly processes, fulfilling a function similar to that of natural selection, which determine whether newly arisen ideas will in fact be perpetuated in future generations or not. How far is the arising of culturally novel ideas a process which can be characterized as random, even in the restricted sense in which we have seen this term should be used in the biological sphere? What is it that determines the intensity of the natural selective pressure for or against the preservation of new ideas? Again, items capable of cultural transmission such as ideas, techniques or skills do not occur in isolation but are found in co-ordinated groups. Can we find here some parallel to the genetic phenomena of linkage and recombination? The cultural exploitive system, the system of choosing and modifying the environment, is also obviously very highly developed. Again, cultures reacting to external stresses may become particularly liable to modification in certain directions, exhibiting phenomena similar to those we have attributed to the epigenetic system. All these parallels, however, remain as yet very incompletely worked out. It would probably be profitable to pursue them[6].

Although it would seem prudent, when faced by a phenomenon of human evolution, first to consider by what cultural means it has been brought about, it is also very necessary to inquire into the biological or genetical phenomena associated with it. This is, however, exceedingly difficult. Suppose a marked change takes place in the gene pool of the human population; under what circumstances should we expect this to have an important influence on the essential cultural achievements of the group concerned? It is extraordinarily difficult to find any factual evidence, since most examples of marked changes in the gene pool of a population involve the immigration or emigration of individuals who carry with them not only their transmissible genes but also their transmissible culture. For example, one may postulate, as Darlington[5] has done, that the emigrants from Ireland in the middle of the past century carried out of the population many genes for various types of socially effective behaviour, leaving the home population impoverished. But in practice the existence of these genes is only hypothetical, and even if they did exist the emigrants also undoubtedly carried with them culturally transmitted tendencies to vigorous behaviour.

There are a few cases, however—for example, when Jewish populations have immigrated into or out of a country, with whose population they have not engaged in extensive cross-breeding, but on whose life they have exerted a considerable influence—in which one may deduce that this influence has been primarily a cultural rather than a genetic one. Even if we were to make the unsafe assumption that it is their genes which endow the Jewish people or the Chinese with great ability in trade, the effect which a small number of Jews or Chinese may have on the economic existence of the people surrounding them can only be the result of cultural rather than genetic transmission. Again, the rapidity, in terms of numbers of generations, with which many steps of evolution take place (such as, say, the formation of the characteristic United States culture out of an extraordinarily mixed European immigrant population) is scarcely compatible with the operations of the genetic evolutionary mechanism and, it would seem, must in the main be attributed to the actions of the human cultural evolutionary system.

When we can discern cultural differences between two human groups, does the main responsibility of these lie with the system of cultural transmission or with that of genetic transmission? Again, from an *a priori* point of view one must expect differences in both systems to be involved, and it is exceedingly difficult to assess the relative importance of the two contributing factors. It is quite clear that races such as the West Africans, the Maoris and the Chinese, differ genetically from Europeans. Some of these genetic differences are obviously expressed in skin colour; there must surely be others, more difficult to detect. But is there any reason, for example, to suppose that it is the differences in the gene pool between the Chinese and the European populations which have caused the one to develop a social system based on such relatively unindividualistic systems as Confucianism and Buddhism and the other a civilization inspired by such a different system of thought and feeling as Christianity? I see no *a priori* reason to suppose anything of the kind; nor is there sufficient factual evidence to establish such a conclusion.

Again, one can find examples, particularly in quite recent times, in which human populations have undergone important changes in periods of time which seem much too short to allow of noteworthy alterations in their genetic endowment. The change in West Africa from the conditions described a century ago, to the present highly sophisticated and technologically competent modern societies, can only have been accompanied by exceedingly small, if any, changes in the general gene pool. One of the most striking of such changes, and one of the very few that has been carefully studied by a highly trained specialist, is that of the Manus people of the Admiralty Islands in the Pacific, studied by Margaret Mead[7]. This transformation from a palæolithic to at least the beginnings of a modern society has taken place within a lifetime; that is to say, it has involved *no* genetic alteration. It is a most remarkable example of how powerful the cultural evolutionary system may be.

These examples suggest, in my opinion, that in producing the changes of the kind which we consider of major importance in the evolution of mankind, the cultural system of transmission usually contributes incomparably more than the genetical. Even when we can be certain that genetical changes have occurred, as, for example, in the comparison between Africans and Europeans, there are only one or two examples in which these changes can be shown to have any practical importance.

The genetic system of a population, as Lerner[8], in particular, has pointed out, shows a considerable power of resistance to factors such as natural or artificial selection which attempt to alter it. I have argued that the epigenetic system shows similar characteristics of unresponsiveness[3]. One might expect, and I think the evidence suggests, that cultural systems also have some tendency to stability. This is probably correlated to some extent with their size. The fantastically rapid transformation of Manus society occurred in a minute population of only a few thousands; one could scarcely expect the fifty millions of Nigeria or the five hundred millions of China to alter as rapidly. One cannot, therefore, always expect the processes of change mediated by the cultural evolutionary system to occur in a shorter time than those which might be carried out by the genetic system. It is only in favourable cases that the critical evidence emerges which shows that steps in human evolution can occur at a rate much faster than the genetic mechanisms could bring about. Cultural phenomena which involve stability over long periods need not necessarily, on *a priori* grounds, be attributed to the genetical system; there is no reason to doubt that cultural transmission may operate over many generations. Such questions will only be answerable when we find further methods of gathering empirical data which will enable us to distinguish the contributions of the two information-transmitting systems in each particular case.

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OBITUARIES

Sir Stanley Angwin, K.C.M.G., K.B.E., D.S.O., M.C.

THE death on April 21 at the age of seventy-five of Sir Stanley Angwin brings to a close a remarkable military and engineering career. Educated at Queen Mary College, he received his practical training with Messrs. Yarrow and Co., the shipbuilders. In 1906, at the age of twenty-three, he entered the Engineering Department of the Post Office, a step which took him in the course of fifty years to the highest engineering and administrative positions in the telecommunications field; he became engineer-in-chief of the Post Office in 1939, chairman of Cable and Wireless in 1947 and finally chairman of the Commonwealth Telecommunications Board from 1951 until 1956.

It was provident that Angwin was engineer-in-chief during the Second World War, for the part played by telecommunications was vital and demanded extreme co-operation with the Fighting Services. Angwin had a foot in both the Civil and Services' camps, for he had been associated with the Army Signals since the inauguration of the Territorial Army. His Unit, which he raised as the Lowland Division Telegraph Company, was mobilized in 1914 to form the 52nd Divisional Signal Company and served throughout the First World War in Gallipoli, Egypt, Palestine and France. He was awarded the D.S.O. and M.C., and those who knew his scant personal regard for air raids in 1940 can readily imagine the value and influence of his imperturbable personality as a young commander in the earlier War. His association with Army Signals continued between the Wars, first in command of the 44th Home Counties Divisional Signals and finally as deputy chief signal officer for the Supplementary Reserve.

With this background, Angwin was in an excellent and accepted position to assess and direct the provision of the many long-distance circuits and installations required for the defence of the United Kingdom. The demands for Post Office services were overwhelming, and sometimes competing, particularly for air defence, and later for the U.S. Armed Forces, and the preparations for *D* Day. All this in the face of bomb damage, and incessant repairs, provided a formidable task of direction, while at the same time Angwin fostered the release of technical staff to the Forces for the build-up of the signal staffs and units overseas where their professional knowledge was indispensable.

Between the Wars Angwin's work had been associated with the development of the Post Office and Commonwealth radio services. On his return from the First World War he was appointed to the wireless section of the Engineer-in-Chief's office. There he found, in an era of development, just those opportunities needed to match his many talents. On the technical side he found scope for applying his knowledge and experience in the design and construction of high-power radio stations at Cairo, Leafield and Rugby; and was closely connected with the establishment in 1927 of the first trans-Atlantic telephone service and in the subsequent development of short-wave radio telephone services to all parts of the world.

Angwin's ability in negotiation was equally outstanding. This frequently led to his appointment as chairman of committees, particularly those dealing with controversial matters, at many international telecommunication conferences.

He was chairman of the Radio Research Board during 1947–52. In 1945 he accompanied Lord Reith on a mission to the members of the Commonwealth to discuss changes in Commonwealth communications, leading to the nationalization of Cable and Wireless, Ltd., and to the setting up of the Commonwealth Telecommunications Board.

On retirement from the Post Office, Angwin became in January 1947 the first chairman of Cable and Wireless, Ltd., in its new role, and in April 1951, at the invitation of the partner Governments, followed Lord Reith as chairman of the Commonwealth Telecommunications Board. In 1950, as chief technical adviser to the Board, he had presided over a meeting of technical and traffic experts from all parts of the Commonwealth, which was the first Commonwealth gathering of its kind. He was chairman of the Board for five years, filling this office with his usual distinction and doing much to further Commonwealth co-operation in all spheres of telecommunications. In 1954 he headed a delegation of the Board to Australia and New Zealand. In 1955 he presided over a second successful technical and traffic conference in London, but in 1956, owing to ill-health, he felt obliged to retire.

As engineer-in-chief of the Post Office, Angwin was knighted in 1941 and made K.B.E. in 1945 for his war services. For his services to international telecommunications he was made K.C.M.G. in 1957. He was president of the Institution of Electrical Engineers during 1943–44, Faraday Medallist in 1953 and made an honorary member in 1956. He became a Fellow of Queen Mary College, London, in 1946