

References and Notes

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- Cholesterol esters of long chain fatty acids can exist in three liquid-like states; a true isotropic liquid state, a cholesteric liquid-crystalline state, or a smectic liquid-crystalline state (4). Each of these liquid-like states can dissolve some cholesterol. The amount dissolved by the liquid phase of cholesteryl linoleate at 37°C is 8 percent by weight. Mixtures of other esters found in atherosclerotic lesions which form liquid or liquid crystalline phases at 37°C also dissolve about 5 to 8 percent of cholesterol by weight.
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- The fact that the oily cholesterol ester phase does not appear to be completely saturated with cholesterol may be related to the conditions under which the phase is isolated. For instance, this phase was isolated at 22°C, a temperature at which cholesterol is less soluble in the oily cholesterol ester phase than it is at 37°C (4).
- We fully realize that this may be an oversimplification. First, cholesterol esters such as cholesteryl palmitate, cholesteryl stearate, and cholesteryl oleate, which are known to exist in plaques (9), have melting points well above 37°C (4) and although these esters may form low-melting eutectics with more highly unsaturated esters [such as the eutectic noted with cholesteryl linoleate-cholesteryl oleate systems (4)] it is possible that some of these esters might exist as crystalline solids in the plaque. Esters in a crystalline form have not, however, been identified in fresh plaques. Second, sphingomyelin can form an ordered phase above 37°C, especially if its proportion to the other membrane phospholipids becomes large. Thus, since sphingomyelin becomes the major phospholipid in advanced lesions it is possible that an ordered phase of sphingomyelin could be formed and be present in the plaque.
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- We thank C. R. Loomis, M. J. Janiak, and Dr. E. Rogers for helpful discussions and Ms. S. Siegel for secretarial assistance. This study was supported by Public Health Service grant AM 11453.

Analogy as a Source of Knowledge

Konrad Z. Lorenz

Concept of Analogy

In the course of evolution it constantly happens that, independently of each other, two different forms of life take similar, parallel paths in adapting themselves to the same external circumstances. Practically all animals which move fast in a homogeneous medium have found means of giving their bodies a streamlined shape, thereby reducing friction to a minimum. The "invention" of concentrating light on a tissue sensi-

tive to it by means of a diaphanous lens has been made independently at least four times by different phyla of animals; and in two of these, in the cephalopods and in the vertebrates, this

kind of "eye" has evolved into the true, image-projecting camera through which we ourselves are able to see the world.

Thanks to old discoveries by Charles Darwin and very recent ones by biochemists, we have a fairly sound knowledge of the processes which, in the course of evolution, achieve these marvelous structures. The student of evolution has good reason to assume that the abundance of different bodily structures which, by their wonderful expediency, make life possible for such amazingly different creatures under such amazingly different conditions, all owe their existence to these processes which we are wont to subsume under

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the concept of adaptation. This assumption, whose correctness I do not propose to discuss here, forms the basis of the reasoning which the evolutionist applies to the phenomenon of analogy.

Deducing Comparable Survival Value from Similarity of Form

Whenever we find, in two forms of life that are unrelated to each other, a similarity of form or of behavior patterns which relates to more than a few minor details, we assume it to be caused by parallel adaptation to the same life-preserving function. The improbability of coincidental similarity is proportional to the number of independent traits of similarity, and is, for n such characters, equal to 2^{n-1} . If

we find, in a swift and in an airplane, or in a shark or a dolphin, and in a torpedo the striking resemblances illustrated in Fig. 1, we can safely assume that in the organisms as well as in the man-made machines, the need to reduce friction has led to parallel adaptations. Though the independent points of similarity are in these cases not very many, it is still a safe guess that any organism or vehicle possessing them is adapted to fast motion.

There are conformities which concern an incomparably greater number of independent details. Figure 2 shows cross sections through the eyes of a vertebrate and a cephalopod. In both cases there is a lens, a retina connected by nerves with the brain, a muscle moving the lens in order to focus, a contractile iris acting as a diaphragm,

a diaphanous cornea in front of the camera, and a layer of pigmented cells shielding it from behind—as well as many other matching details. If a zoologist who knew nothing whatever of the existence of cephalopods were examining such an eye for the very first time, he would conclude without further ado that it was indeed a light-perceiving organ. He would not even need to observe a live octopus to know this much with certainty.

The Allegation of "False Analogy"

Ethologists are often accused of drawing false analogies between animal and human behavior. However, no such thing as a false analogy exists: An analogy can be more or less detailed and hence more or less informative. Assiduously searching for a really false analogy, I found a couple of technological examples within my own experience. Once I mistook a stern wheeler steamer for a ship mill. A vessel was anchored on the banks of the Danube near Budapest. It had a little smoking funnel and at its stern an enormous slowly turning paddle wheel. Another time, I mistook a small electric power plant, consisting of a two-stroke engine and a dynamo, for a compressor. The only biological example that I could find concerned a luminescent organ of a pelagic gastropod, which was mistaken for an eye because it had an epidermal lens and, behind this, a high cylindrical epithelium connected with the brain by a nerve. Even in these examples, the analogy was false only with respect to the direction in which energy was transmitted.

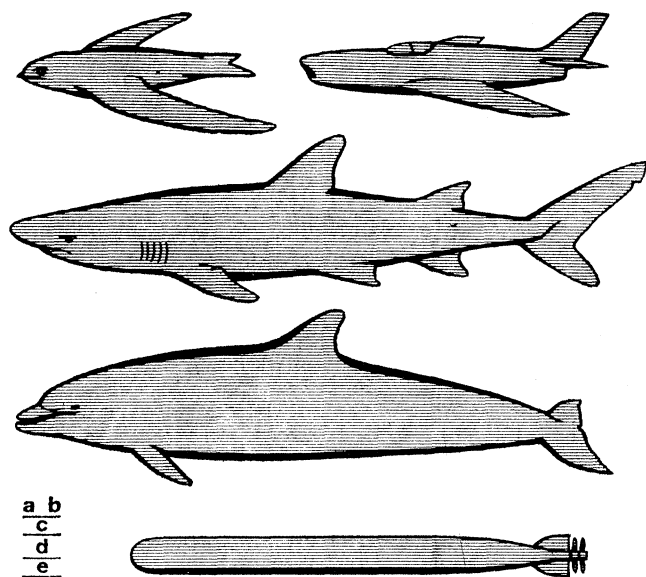


Fig. 1. Analogy of form due to adaptation to an identical function. Streamlining in (a) a swift, (b) a fighter plane, (c) a shark, (d) a dolphin, and (e) a torpedo.

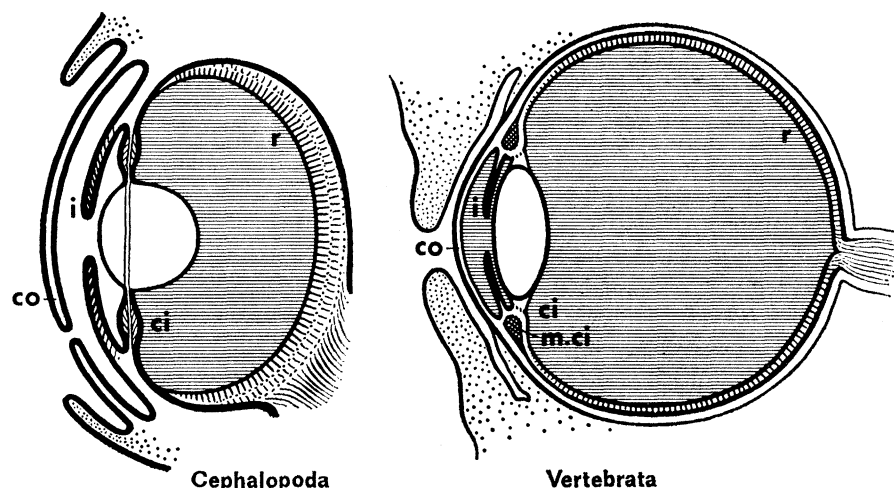


Fig. 2. Detailed analogy in two independently evolved light-perceiving organs. (Left) the eye of an octopus; (right) the eye of a man; co, cornea; ci, corpus ciliare; m.ci, musculus ciliaris; i, iris; r, retina.

The Concept of Homology

There is, in my opinion, only one possibility of an error that might conceivably be described as the "drawing of a false analogy" and that is mistaking a homology for an analogy. A homology can be defined as any resemblance between two species that can be explained by their common descent from an ancestor possessing the character in which they are similar to each other. Strictly speaking, the term homologous can only be applied to characters and not to organs. Figure 3 shows the forelimbs of a number of tetrapod vertebrates intentionally chosen to illustrate the extreme variety of uses to which a

front leg can be put and the evolutionary changes it can undergo in the service of these different functions. Notwithstanding the dissimilarities of these functions and of their respective requirements, all these members are built on the same basic plan and consist of comparable elements, such as bones, muscles, and nerves. The very dissimilarity of their functions makes it extremely improbable that the manifold resemblances of their forms could be due to parallel adaptation—in other words, to analogy.

As a pupil of the comparative anatomist and embryologist Ferdinand Hochstetter, I had the benefit of a very thorough instruction in the methodological procedure of distinguishing similarities caused by common descent from those due to parallel adaptation. In fact, the making of this distinction forms a great part of the comparative evolutionist's daily work. Perhaps I should mention here that this procedure has led me to the discovery which I personally consider to be my own most important contribution to science. Knowing animal behavior as I did, and being instructed in the methods of phylogenetic comparison as I was, I could not fail to discover that the very same methods of comparison, the same concepts of analogy and homology, are as applicable to characters of behavior as they are in those of morphology. This discovery is implicitly contained in the works of Charles Otis Whitman and of Oskar Heinroth; it is only its explicit formulation and the realization of its far-reaching inferences to which I can lay claim. A great part of my life's work has consisted in tracing the phylogeny of behavior by disentangling the effects of homology and of parallel evolution. Full recognition of the fact that behavior patterns can be hereditary and species-specific to the point of being homologizable was impeded by resistance from certain schools of thought, and my extensive paper on homologous motor patterns in Anatidae was necessary to make my point.

Cultural Homology

Much later in life I realized that, in the development of human cultures, the interaction between historically induced similarities and resemblances caused by parallel evolution—in other words, between homologies and analogies—was very much the same as in the phylog-

eny of species and that it posed very much the same problems. I shall have occasion to refer to these later on; here I want to illustrate the existence of cultural homology. Figure 4 illustrates the cultural changes by which the piece of medieval armor that was originally designed to protect throat and chest was gradually turned, by a change of function, into a status symbol. Otto Koenig, in his book *Kulturethologie*, has adduced many other examples of persistent historically induced similarity of characters to which the adjective "homologous" can legitimately be applied.

Ritualization and symbolisms play a role in traditional clothing and particularly in military uniforms in their historical changes, so that the appearance of historically retained similarities is, perhaps, not very surprising. It is, however, surprising that the same retention of historical features, not only independently of function, but in clear defiance of it, is observable even in that part of human culture which one would suppose to be free of symbolism, ritualization, and sentimental conserva-

tivism—namely, in technology. Figure 5 illustrates the development of the railway carriage. The ancestral form of the horse-drawn coach stubbornly persists despite the very considerable difficulties which it entails, such as the necessity of constructing a running-board all along the train, on which the conductor had to climb along, from compartment to compartment, exposed to the inclemency of the weather and to the obvious danger of falling off. The advantages of the alternative solution of building a longitudinal corridor within the carriage are so obvious that they serve as a demonstration of the amazing power exerted by the factors tending to preserve historical features in defiance of expediency.

The existence of these cultural homologies is of high theoretical importance, as it proves that, in the passing-on of cultural information from one generation to the next, processes are at work which are entirely independent of rational considerations and which, in many respects, are functionally analogous to the factors maintaining invariance in genetical inheritance.

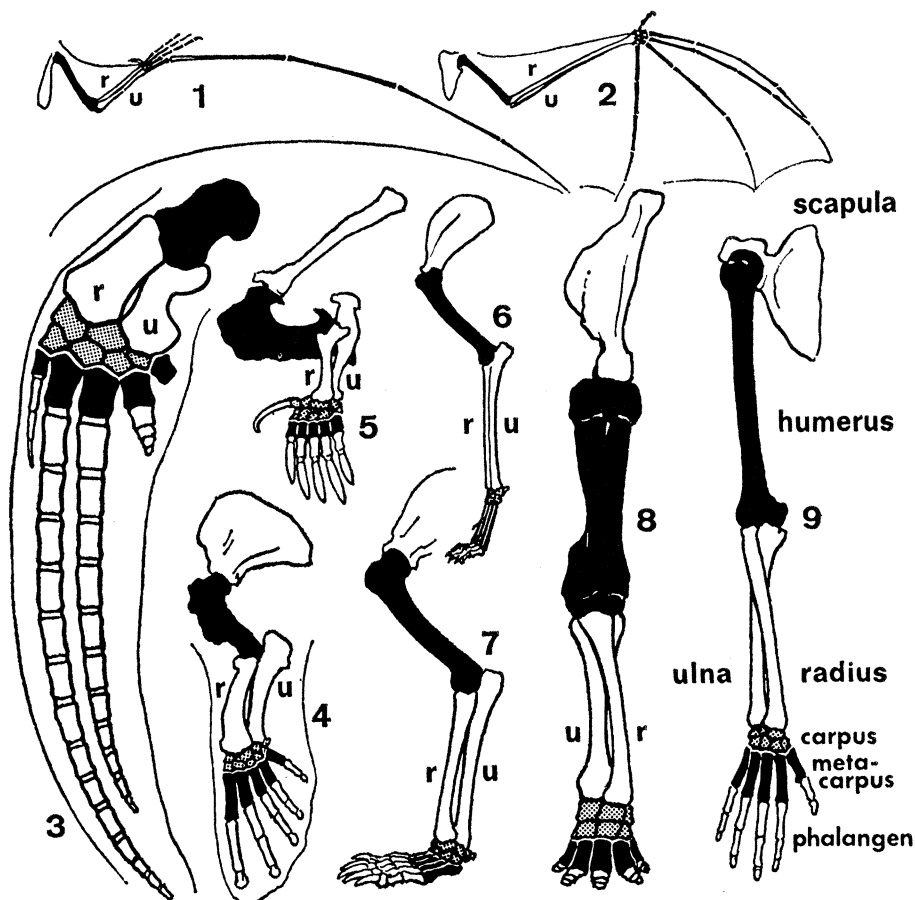


Fig. 3. Anterior limbs of vertebrates. (1) Jurassic flying reptile; (2) bat; (3) whale; (4) sea lion; (5) mole; (6) dog; (7) bear; (8) elephant; and (9) man. The humerus and the metacarpal bones are tinged in black, the carpal bone in grey.

Deducing Function from Behavioral Analogies

Let me now speak of the value of analogies in the study of behavior. Not being vitalists, we hold that any regularly observable pattern of behavior which, with equal regularity, achieves survival value, is the function of a sensory and nervous mechanism evolved by the species in the service of that par-

ticular function. Necessarily, the structures underlying such a function must be very complicated, and the more complicated they are, the less likely it is, as we already know, that two unrelated forms of life should, by sheer coincidence, have happened to evolve behavior patterns which resemble each other in a great many independent characters.

A striking example of two complicated sets of behavior patterns evolving

independently in unrelated species, yet in such a manner as to produce a great number of indubitable analogies, is furnished by the behavior of human beings and of geese when they fall in love and when they are jealous. Time and again I have been accused of uncritical anthropomorphism when describing, in some detail, this behavior of birds and people. Psychologists have protested that it is misleading to use terms like falling in love, marrying, or being jealous when speaking of animals. I shall proceed to justify the use of these purely functional concepts. In order to assess correctly the vast improbability of two complicated behavior patterns in two unrelated species being similar to each other in so many independent points, one must envisage the complication of the underlying physiological organization. Consider the minimum degree of complication which even a man-made electronic model would have to possess in order to simulate, in the simplest possible manner, the behavior patterns here under discussion. Imagine an apparatus, A, which is in communication with another one, B, and keeps on continuously checking whether apparatus B gets into communication with a third apparatus, C, and which, furthermore, on finding that this is indeed the case, does its utmost to interrupt this communication. If one tries to build models simulating these activities, for example, in the manner in which Grey-Walter's famous electronic tortoises are built, one soon realizes that the minimum complication of such a system far surpasses that of a mere eye.

The conclusion to be drawn from this reasoning is as simple as it is important. Since we know that the behavior patterns of geese and men cannot possibly be homologous—the last common ancestors of birds and mammals were lowest reptiles with minute brains and certainly incapable of any complicated social behavior—and since we know that the improbability of coincidental similarity can only be expressed in astronomical numbers, we know for certain that it was a more or less identical survival value which caused jealousy behavior to evolve in birds as well as in man.

This, however, is all that the analogy is able to tell us. It does not tell us wherein this survival value lies—though we can hope to ascertain this by observations and experiments on geese. It does not tell us anything about the physiological mechanisms bringing about jealousy behavior in the two species;

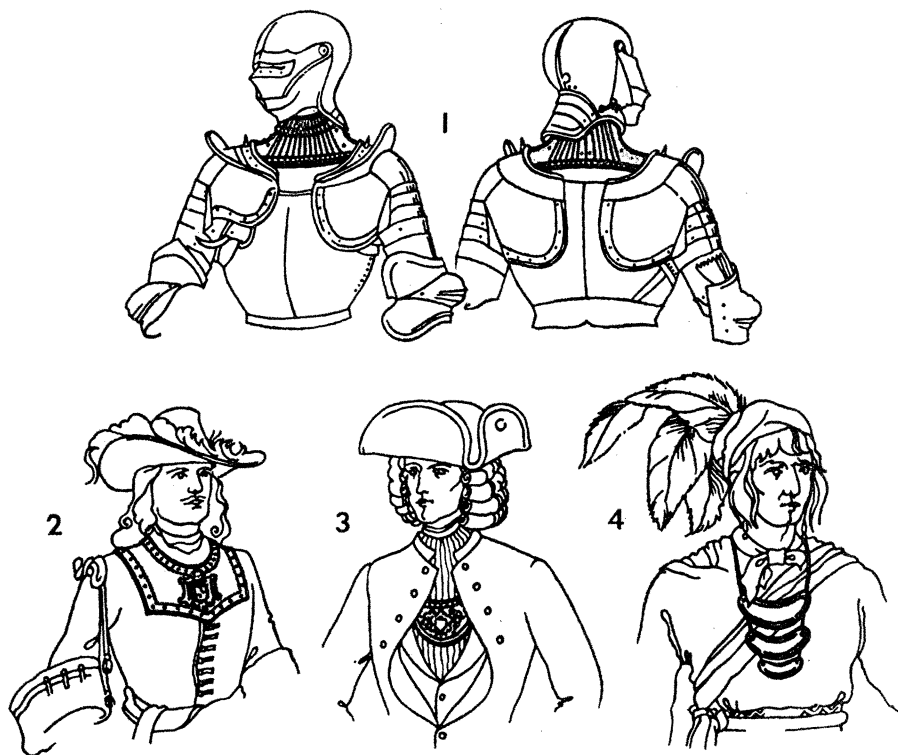


Fig. 4. Change of function in a piece of medieval armor which, losing its protective function, becomes a status symbol of officers.

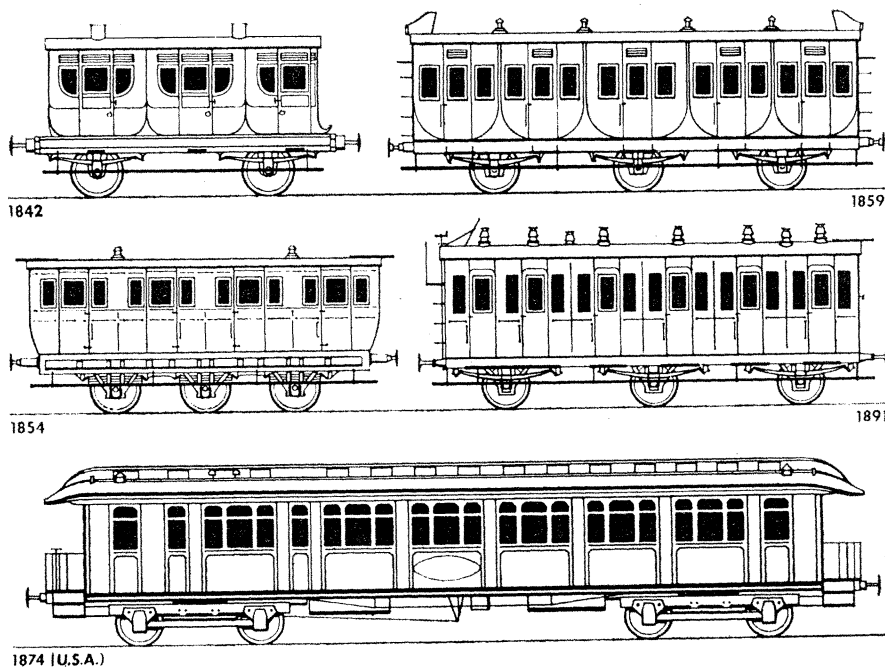


Fig. 5. Homology of technical products. Characters traceable to the ancestor, the horse-drawn coach persists, against the interests of technical progress, in railway carriages.

they may well be quite different in each case. Streamlining is achieved in the shark by the shape of the musculature, in the dolphin by a thick layer of blubber, and in the torpedo by welded steel plates. By the same token, jealousy may be—and probably is—caused by an inherited and genetically fixed program in geese, while it might be determined by cultural tradition in man—though I do not think it is, at least not entirely.

Limited though the knowledge derived from this kind of analogy may be, its importance is considerable. In the complicated interaction of human social behavior, there is much that does not have any survival value and never had any. So it is of consequence to know that a certain recognizable pattern of behavior does, or at least once did, possess a survival value for the species; in other words, that it is not pathological. Our chances of finding out wherein the survival value of the behavior pattern lies are vastly increased by finding the pattern in an animal on which we can experiment.

When we speak of falling in love, of friendship, personal enmity, or jealousy in these or other animals, we are not guilty of anthropomorphism. These terms refer to functionally determined concepts, just as do the terms legs, wings, eyes, and the names used for other bodily structures that have evolved independently in different phyla or animals. No one uses quotation marks when speaking or writing about the eyes or the legs of an insect or a crab, nor do we when discussing analogous behavior patterns.

However, in using these different kinds of terms, we must be very clear as to whether the word we use at a given moment refers to a concept based on functional analogy or to one based on homology, for example, on common phyletic origin. The word “leg” or “wing” may have the connotation of the first kind of concept in one case and of the second in another. Also, there is the third possibility of a word connoting the concept of physiological, causal identity. These three kinds of conceptualization may coincide or they may not. To make a clear distinction between them is particularly important when one is speaking of behavior. A homologous behavior pattern can retain its ancestral form and function in two descendants, and yet become physiologically different. The rhythmical beat of the umbrella is caused by endogenous stimulus generation in many hy-

drozoa and in larva (ephyrae) in other medusae. In adult Scyphomedusae, however, it is caused by reflexes released through the mechanism of the so-called marginal bodies. A homologous motor pattern may retain its original physiological causation as well as its external forms, yet undergo an entire change of function. The motor pattern of “inciting” that is common to the females of most Anatidae is derived from a threatening movement and has the primary function of causing the male to attack the adversary indicated by the female’s threat. It has entirely lost this function in some species, for instance in the goldeneyes, in which it has become a pure courtship movement of the female. Two nonhomologous motor patterns of two related species may, by a change of function, be pressed into the service of the same survival value. The preflight movement of ducks is derived from an intention movement of flying, an upward thrust of head and neck, while the corresponding signal of geese is derived from a displacement shaking of the head. When we speak of “preflight movements of Anatidae” we form a functional concept embracing both. These examples are sufficient to demonstrate the importance of keeping functional, phylogenetical, and physiological conceptualizations clearly apart. Ethologists are not guilty of “reifications” or of illegitimate anticipations of physiological explanations when they form concepts that are only functionally defined—like, for instance, the concept of the IRM, the innate releasing mechanism. They are, in fact, deeply aware that this function may be performed by the sensory organ itself—as in the cricket—or by a complicated organization of the retina—as in the frog—or by the highest and most complicated processes within the central nervous system.

Deducing Physiological Mechanisms from Known Analogous Functions

Recognizing analogies can become an important source of knowledge in quite another way. We can assume with certainty that, for instance, the functions of respiration, of food intake, of excretion, of propagation, and so forth, must somehow be performed by any living organism. In examining an unknown living system, we are, therefore, justified in searching for organs serving functions which we know to be indispensable. We are surprised if we miss some of them; for instance, the respira-

tory tract in some small salamanders which breathe exclusively through their skin.

A human culture is a living system. Though it is one of the highest levels of integration, its continuance is nevertheless dependent on all the indispensable functions mentioned above. The thought obtrudes itself that there is one of these necessary functions which is insufficient in our present culture, that of excretion. Human culture, after enveloping and filling the whole globe, is in danger of being killed by its own excretion, of dying from an illness closely analogous to uremia. Humanity will be forced to invent some sort of planetary kidney—or it will die from its own waste products.

There are other functions that are equally indispensable to the survival of *all* living systems, ranging from bacteria to cultures. In any of these systems, adaptation has been achieved by the process, already mentioned, which hinges on the gaining of information by means of genetic change and natural selection, as well as on the storing of knowledge in the code of the chain molecules in the genome.

This storing, like any retention of information, of knowledge, is achieved by the formation of structure. Not only in the little double helix, but also in the programming of the human brain, in writing, or any other form of “memory bank,” knowledge is laid down in structures.

The indispensable supporting and retaining function of structure always has to be paid for by a “stiffening,” in other words, by the sacrifice of certain degrees of freedom. The structure of our skeleton provides an example; a worm can bend its body at any point, whereas we can flex our limbs only where joints are provided; but we can stand upright and the worm cannot.

All the adaptedness of living systems is based on knowledge laid down in structure; structure means static adaptedness, as opposed to the dynamic process of adaptation. Hence, new adaptation unconditionally presupposes a dismantling of some structures. The gaining of new information inexorably demands the breaking down of some previous knowledge which, up to that moment, had appeared to be final.

The dynamics of these two antagonistic functions are universally common to all living systems. Always, a harmonious equilibrium must be sustained between, on the one hand, the factors maintaining the necessary de-

gree of invariance and, on the other, the factors which tend to break up firm structures and thereby create the degree of variability which is the prerequisite of all further gaining of information, in other words, of all new adaptation.

All this is obviously true of human culture as well as of any other living system whose life-span exceeds that of the individual, for example, of any species of bacteria, plants, or animals. It is, therefore, legitimate to search for the mechanisms which, in their harmonious antagonism of preserving and dismantling structures, achieve the task of keeping a culture adapted to its ever-changing environment. In my latest book *Die Rückseite des Spiegels*, I have tried to demonstrate these two antagonistic sets of mechanisms in human culture.

The preservation of the necessary invariance is achieved by procedures curiously reminiscent of genetic inheritance. In much the same manner as the new nucleotides are arranged along the old half of a double helix, so as to produce a copy of it, the invariant structures of a culture are passed on, from one generation to the next, by a process in which the young generation makes a

copy of the cultural knowledge possessed by the old. Sheer imitation, respect for a father figure, identification with it, force of habit, love of old ritualized customs, and, last but not least, the conservatism of "magical thinking" and superstition—which as we have seen influences even the construction of railway carriages—contributes to invest cultural tradition with that degree of invariance which is necessary to make it inheritable at all.

Opposed to these invariance-preserving mechanisms, there is the specifically human urge to curiosity and freedom of thought which, with some of us, persists until senescence puts a stop to it. However, the age of puberty is typically the phase in our ontogeny during which we tend to rebel against tradition, to doubt the wisdom of traditional knowledge and to cast about for new causes to embrace, for new ideals.

In a paper which I read a few years ago—at a Nobel symposium on "The place of value in a world of facts"—I tried to analyze certain malfunctions of the antagonistic mechanisms and the dangers of an enmity between the generations arising from these disturbances. I tried to convince my audience that the question whether conservatism is

"good" or "bad," or whether the rebellion of youth is "good" or "bad," is just as inane as the question whether some endocrine function, for instance that of the thyroid gland, is "good" or "bad." Excesses as well as deficiency of any such function cause illness. Excess of thyroid function causes Basedow's disease, deficiency myxedema. Excess of conservatism produces living fossils which will not go on living for long, and excess of viability results in the appearance of monsters which are not viable at all.

Between the conservative representatives of the "establishment" on the one hand and rebelling youth on the other, there has arisen a certain enmity which makes it difficult for each of the antagonists to recognize the fact that the endeavours of both are equally indispensable for the survival of our culture. If and when this enmity escalates into actual hate, the antagonists cease to interact in the normal way and begin to treat each other as different, hostile cultures; in fact they begin to indulge in activities closely akin to tribal warfare. This represents a great danger to our culture, inasmuch as it may result in a complete disruption of its traditions.

NEWS AND COMMENT

Sahelian Drought: No Victory for Western Aid

The famine that struck the six Sahelian zone countries of West Africa last year is thought to have killed some 100,000 people and left 7 million others dependent on foreigners' food handouts. The same or worse may happen again this year. The essence of the tragedy is that the famine was caused not by dry weather or some putative climatic change but, primarily, by man himself. Could not Western skills, applied in time, have saved the primitive nomads and slash-and-burn farmers from destroying their own land? Western intervention in the Sahel, Western science and technology, and the best intentioned efforts of donor agencies and governments over the last several decades, have in fact made a principal contribution to the destruction.

"One of the basic factors in the

situation is overpopulation, both human and bovine, brought about by the application of modern science," says a former Food and Agricultural Organization (FAO) sociologist. According to a recent in-house report on the Sahel prepared by the Agency for International Development (AID), "To a large extent the deterioration of the subsistence base is directly attributable to the fact that man's interventions in the delicately balanced ecological zones bordering desert areas have usually been narrowly conceived and poorly implemented." "Too many of our projects have been singularly unproductive and . . . we have tediously reintroduced projects which ought never to have been attempted in the first place," says Michael M. Horowitz, a State University of New York anthropologist who has studied the nomad peoples of Niger.

And, to quote the AID report again, "It must be recognized that assistance agencies have ignored the principles [of effective resource management], and the consequence of indiscriminate support has produced negative results or, on occasion, disaster."

The symptoms of distress in the Sahel are easier to perceive than the underlying causes of the disaster. The six countries concerned—Senegal, Mauritania, Mali, Upper Volta, Niger, and Chad—are former French colonies that stretch along the southern edge of the Sahara desert. The land is mostly semi-desert that enjoys only 4 months of rainfall a year. But the grasses are sufficient to support the herds of cattle tended by the nomads, and in the southern regions millet and sorghum are grown, together with cash crops such as peanuts and cotton. By 1970, just before the collapse, the fragile steppe and savannah ecology of the six countries was supporting some 24 million people and about the same number of animals. This burden amounted to roughly a third more people and twice as many animals as the land was carrying 40 years ago.

The agent of collapse was a drought