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STATISTICAL AND HIERARCHICAL ASPECTS OF BIOLOGICAL ORGANIZATION

Michael Conrad

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Center for Theoretical Studies

Coral Gables, Florida 33124

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Abstract

Biological organization has a compartmental structure. The organization and variability of these compartments, or the degree of differentiation and uncertainty associated with them, are expressed in terms of certain entropy measures. Uncertainty is related to the adaptability of the compartment. The condition for most efficient operation of biological systems is discussed in these terms, as are various processes, such as computation, control, and competition. A principle of static equilibrium is proposed, according to which the uncertainty associated with the system approaches the uncertainty associated with the environment, including other biological systems. This is represented in terms of a vector model of biological organization. The relation only expresses conditions which biological systems tend to fulfill in the course of evolution. However, this makes it useful to treat the uncertainty associated with the biological system as a whole as an approximately conserved quantity. The distribution of variability to different levels of organization is discussed on this basis, and the model is compared to the background of biological fact.

I. Introduction

Biological nature has a compartmental structure. For example, consider an ecosystem in the most general sense--as the aggregate of all the components of a complete biological system. The ecosystem could be thought of in terms of the configuration of certain fundamental components--say small molecules. However, this would obscure the organization of the ecosystem. In fact, biologists have found it useful to describe the ecosystem as a configuration of species, species as configurations of organisms, organisms as configurations of cells, and so forth.

Each of these compartments has certain intrinsic relations and certain extrinsic relations. The intrinsic relations, or pattern of interconnection of components, determines how the compartment works. The extrinsic relations determine why the compartment works in this way. Thus, intrinsic and extrinsic relations of a compartment are not independent, in the sense that "why" questions at one level of organization are "how" questions at a higher level of organization.

The compartments of a biological system, except for single molecules, are open to materials which cycle through the ecosystem. Compartments are also open to energy, which is converted to lower grade energy. There are many alternative pathways by which high grade energy may be converted to lower grade energy. It is these alternatives which provide the basis for information processing in biology. The compartments, at the cellular level and above, are self-reproducing. Such systems must have a description or genotype, as well as decoding machinery. The description codes for the sequence

of amino acids in proteins. These proteins, in turn, select the pattern of pathways which characterize the system.

Whether or not a compartment actually reproduces depends on its physical and biological environment--on the conformation of the ecosystem. In order to reproduce a compartment must be specialized, or adapted to its environment. The compartment must also be adaptable, or capable of coping with an uncertain environment. Adaptability is related to the ensemble of possible configurations of a compartment, or its possible modes of behavior. The adaptability and adaptedness of a compartment may interfere with one another, in the sense that an increase in the ensemble of configurations entails a decrease in the specific relationship between the system and any given environment. Furthermore, the relations between compartments at different levels of organization may result in cross level interference effects.

Each compartment of a biological system is more or less specialized, or more or less adaptable, in the sense of being associated with a larger or smaller ensemble of configurations. For example, the gene pool may be more or less diverse, developmental patterns more or less plastic, control mechanisms at the cellular, organismic, and societal levels more or less homeostatic, behavior patterns at the neural level more or less instinctive. A biological system has form, in the sense that these statistical or control characteristics are allocated to compartments in a certain way.

In this paper I would like to consider some of the factors which determine this form. In particular, I will consider a relation which ties the compartments of a biological system together,

in the sense of imposing certain restrictions on its form. This relation connects the control, computation, coding, and variability characteristics of biological systems to the noise characteristics of the environment, at least to the extent of expressing tendencies which might be expected in the course of evolution.

The approach which will be followed is along the lines of information theory, and is based on the work of Shannon (1962) and Ashby (1956), but I should also mention papers of Pattee (1969, 1970), Cowan and Winograd (1963), Levins (1968), Lewontin (1961), and Margelef (1953). I will begin by considering the structure of biological organization. Then I will define statistical quantities which can be associated with adaptability and specialization, and will consider the specialization of labor in biological systems. This will provide a basis for discussing the relation between the statistical characteristics of a biological system and its environment, as well as the distribution of these characteristics to different compartments. These relations will be expressed in the form of a vector representation of biological organization. In the final sections I will develop a simple model of biological organization and will discuss (in terms of the model) some of the facts which have motivated the present approach.

II. Compartmental Structure of Biological Organization

Let ${}^{h}_{k}c^{j}_{i}$ represent compartment i at level j of compartment k at level h. For example, some cell could be compartment i of organism k. In general indices will be suppressed when they are not needed.

We would like to partition the ecosystem into compartments such that at any given time no molecule is in more than one compartment at a given level. That is, compartments must be nonintersecting as far as their subcompartments are concerned. In this way the variability of each compartment will be counted once only, assuming that the behavior of the system is unaffected by the method of classification. In practice it is likely that the statistical characteristics of a system will be related to the way it is examined.

There are many classification schemes which fulfill the above criterion. However, only certain systems, or units of organization, are interesting from the biological point of view. Compartments are generally chosen in such a way as to minimize the importance of extrinsic relations--that is, on the basis of their relative degree of isolation.

A possible classification is listed in Table 1. The main levels include cells, organisms, and species. In practice it is quite difficult to define these units precisely. However, each cell has a description, encoded in nucleic acid molecules. An organism is a society of cells, each deriving from a single cell. Similarly, the species is a lineage of organisms which share a common gene pool, in the sense that they can exchange information embodied in their descriptions. Each of these compartments may have certain specialized subregions or organs: trophic structure in the ecosystem; social organization within the species; organs proper in the organisms; organelles, including the genome, in cells.

Table 1

Possible Classification of Biological Organization

level (j)	compartment
7	ecosystem
6	trophic level
5	species or society
4	organism
3	organ
2	cell
1	organelle or large molecule
0	small molecule

The classification is not entirely satisfactory, since it does not eliminate certain important relations between compartments. For example, the structure of the gene pool may be described at the level of the genome, not at the level of the species. The species is included because the top level of the ecosystem is usually described in terms of species relationships, where species are defined on a typological basis. In the present classification the configuration of the species is associated with social organization. However, the inclusion of species precludes the inclusion of social organizations involving symbiosis. These must be included in the description of the ecosystem at the top level. Actually, it may be convenient to describe the ecosystem in terms of relationships between trophic levels, including grazing and detritus pathways, as well as pathways of material not bound in organic form.

III. States of Compartments

Each compartment has states. The states are configurations of subcompartments at some lower level. For example, the organism has states--these are configurations of organs; organs have states--these are configurations of cells, and so forth. In general the state of compartment c_i^j is determined by the configuration of the ${}_i^j c_k^h$, the subcompartments at level h. Unless otherwise specified the state of a compartment will be determined by the configuration of compartments at the next lower level (h=j-1). The set of states associated with each compartment will be denoted by capital letters and the individual states by small letters. For example, the set of system states is represented by S ($s_\alpha \in S$) and the set of environmental states by S* ($s^*_\alpha \in S^*$). The set of states associated with compartment c_i^j is S_i^j, with $s_{i_\beta}^j \in S_i^j$. The state set of all compartments of the system other than c_i^j will be denoted by $\bar{S}_i^j$, with $\bar{s}_{i_\gamma}^j \in \bar{S}_i^j$. Notice that we can identify s_α with the pair $(s_{i_\beta}^j, \bar{s}_{i_\gamma}^j)$ for some α.

Suppose that S_i^j are states of interest, associated with some compartment of interest. The compartment is exposed to certain environmental states or external inputs, represented by S*. The compartment may also be influenced by complementary states or controlling inputs from other compartments, represented by $\bar{S}_i^j$. The complementary compartments of a system are just those which are not included in the description of the compartment of interest, whether or not they are at the same level of organization. Of course the decomposition of a system into complementary compartments and compartments of interest is a matter of viewpoint. Environmental states are those over which a system has very little influence,

at least in the short run.

The map

$$M: S^*(t) \times \bar{S}_i^j(t) \rightarrow S_i^j(t+\tau) \tag{1}$$

represents the matrix

	$\bar{s}_{i_1}^j(t) \ldots\ldots \bar{s}_{i_m}^j(t)$
$s_1^*(t)$	$s_{i_{11}}^j(t+\tau) \ldots\ldots s_{i_{m1}}^j(t+\tau)$
.	. .
.	. .
.	. .
.	. .
.	. .
.	. .
$s_n^*(t)$	$s_{i_{1n}}^j(t+\tau) \ldots\ldots s_{i_{mn}}^j(t+\tau)$

(2)

where t is the time, τ is some time interval, and $s_{i_{uv}}^j = s_{i_\alpha}^j$ for some α.

For example,

$$B: S^*(t) \times S(t) \rightarrow S(t+\tau) \tag{3}$$

represents the transformations of a complete biological system since there are no complementary compartments. As another example, consider

$$a: S^*(t) \times \bar{S}_i^j(t) \rightarrow \bar{S}_i^j(t+\tau_a) \tag{4}$$

$$b: S^*(t) \times \bar{S}_i^j(t) \rightarrow S_i^j(t+\tau_b) \; . \tag{5}$$

Formally, this defines an automaton, where the complementary states

provide a memory capacity allowing constrained or programmed behavior. (See, for example, Arbib, 1964). The complementary states could also be affected by direct feedback from the states of interest,

$$c: \bar{s}_i^j(t) \times s_i^j(t) \rightarrow \bar{s}_i^j(t+\tau_c) \ . \qquad (6)$$

If τ_a or τ_c is less than τ_b, the state $s_{i_\beta}^j$ appearing in map b can be controlled to a high degree of accuracy.

In the following discussion we will consider maps of type b. These do not provide a complete description of a biological system. However, maps such as a and c will be subsumed in certain terms which are used to describe b.

A system may have an equivalence class of histories, in the sense that the future state is not uniquely determined by the present state and environment. For example, $s_{i_{uv}}^j$ may be the same as $s_{i_{uw}}^j$ in the matrix representing b (or M). Such selective loss of information about the past is an essential requirement for machine behavior. (Minsky, 1967; Winograd and Cowan, 1963). This is evident from the fact that most computations cannot be performed without reset operations. In general, any finite automaton can be decomposed into simple reversible and simple irreversible machines, or actually into the groups and semigroups associated with these (Khron and Rhodes, 1963).

A purely mechanical system is reversible, since a complete knowledge of a small part of its trajectory determines the past and future uniquely. Thus, loss of information about environmental states must be associated with loss of detailed information about complementary states, assuming that states of interest are completely

specified and that the environmental states are really part of the initial conditions. This is unavoidable if distinct complementary states are indistinguishable, or groupable into classes, from the macroscopic point of view. Accordingly, the processes of computation are dissipative, or thermodynamically irreversible (Pattee, 1969).

IV. Diversity of States

In this section I will discuss a quantity which expresses the uncertainty associated with an ensemble of states, or the diversity of states and their homogeneity of distribution. It is important to distinguish between such uncertainty, which amounts to variability of the compartment, and the diversity and homogeneity of a compartment in terms of its subcompartments. As will be discussed in section VI, the composition of a compartment might be uncertain in this respect without being variable.

Uncertainty is measured by the entropy

$$\Gamma(S_i^j) = - \sum_\beta f(s_{i_\beta}^j) \log_2 f(s_{i_\beta}^j) \qquad (7)$$

where $\Gamma(S_i^j)$ is the state entropy of compartment c_i^j in bits and $f(s_{i_\beta}^j)$ is the frequency of states $s_{i_\beta}^j$. The number of bits represents the number of binary choices required to specify the state of a system. This increases with increase in the number of states (diversity) and equalization of the frequency of states (homogeneity). If the states are not discrete the phase space of the compartment must be divided into cells, and the entropy determined from the frequency with which these cells are occupied. The choice of cell size affects the value of the entropy only through a constant term.

If the system has certain definite trajectories, or sequences of states, these should be classed together as single states. This is necessary since only the frequencies of the sequences contribute to the uncertainty associated with the ensemble.

The frequencies represent similar compartments at different times or stages of development. In this case the entropy characterizes the average uncertainty associated with the system. As a consequence, details about different stages of development are lost, unless separate averages are used for each stage. This reduces difficulties which might arise from memory or non-ergodic properties of individual compartments.

Conditional entropies are also defined. For example

$$\Gamma(\bar{s}_i^j|S^*) = - \sum_{\alpha,\beta} f(\bar{s}_{i_\beta}^j, s_\alpha^*) \log_2 f(\bar{s}_{i_\beta}^j|s_\alpha^*) \tag{8}$$

where $f(\bar{s}_{i_\beta}^j|s_\alpha^*)$ is the frequency of $\bar{s}_{i_\beta}^j$ given the environmental state. In this case the conditional entropy is sometimes called the noise entropy, assuming that information acquired from the environment is being transmitted to the complementary compartment.

Acquired information equals initial uncertainty minus final uncertainty

$$I = \Gamma_{initial} - \Gamma_{final} \tag{9}$$

where I represents information. The point of view is somewhat different in information theory and thermodynamics. In the latter

$$S = - kH \tag{10}$$

where S is here the entropy and H is a quantity which must always decrease (H theorem). k is the Boltzmann constant. Suppose that Γ is expressed on a thermodynamic scale and that the initial entropy is taken as zero.

$$I = -\Gamma_{final} = -S_{final} = H \tag{11}$$

Thus information must always decrease. In information theory the final entropy is ordinarily taken as zero (the state is completely specified).

$$I = \Gamma_{initial} = S_{initial} = -H \tag{12}$$

Here it seems as if information can increase. However, the increase is regarded as noise. (The usual convention in information theory reverses the sign of H).

Entropy, as defined in equation 7, is a statistical measure of spread, without any necessary connection to thermodynamics. According to equation 9, however, information is a negative term in the entropy (Brillouin, 1962). It should be emphasized that the properties of the two quantities may be quite different.

Thermodynamic entropy is proportional to the macroscopic symmetry of a system. From the microscopic point of view a large number of configurations may be consistent with some macroscopic condition. At equilibrium--when macroscopic symmetry is as great as possible consistent with the constraints--most of these configurations are equivalent in terms of the properties characterizing the system, or are associated with small fluctuations. This is the

reason why average values (constructed a priori with the help of an ignorance postulate) represent thermodynamic quantities.

The situation is quite different when flexible constraints are important. For example, in a biological system or computer the inequivalent states predominate. Many such states may be compatible with a given energy condition. In fact, it is this which forms the basis of the behavioral diversity of biological systems. The state entropy is determined from the frequencies of inequivalent states, or states with macroscopically distinguishable effects. An ignorance postulate would rarely be justified apropros such frequencies--ordinarily the state entropy must be determined on an a posteriori basis, requiring the degradation of identically prepared compartments.

The equivalent states also play a role, since they provide the system with a selective independence of initial conditions.

Whether or not the macroscopic diversity makes a significant contribution to thermodynamic entropy is not clear. This point is not really too important in the context of the present discussion, as will be seen in the next section.

V. Least Entropy: Principle of Specialization

In this section I will consider the relationship between the entropy of a system and the efficiency with which it can perform work, where efficiency is the ratio of the actual amount of work performed to the maximum amount that can be performed. It is important to distinguish between thermodynamic entropy, associated with the microscopic ensemble, and state entropy, associated with

the macroscopic ensemble. The work capacity of a biological system will certainly be greater if the ensemble of microscopic states is smaller (least thermodynamic entropy). The efficiency may also be greater if the ensemble of maroscopic states is smaller (least state entropy). In the remainder of this section I will try to show that this is plausible and a matter of experience.

> A decrease in the state entropy of an ensemble, by an appropriate contraction, can increase the efficiency with which the ensemble performs work.

The ensemble is a set of systems. Selection contracts an ensemble by bringing forth some of the constituent systems. The ensemble might also be a single system, in which case contraction means that a new system is brought forth, but with fewer possible configurations. Not every contraction is appropriate, in the sense that the systems selected may or may not be more efficient.

Least state entropy follows if it is assumed that different types of systems cannot be equally well adapted to the same environment, in the sense of performing a given type of work with equal efficiency. For example, according to Gausse's hypothesis distinct species cannot coexist in the same niche. I will assume that this competitive exclusion principle applies to compartments at all levels of biological organization. Thus, compartments of different design usually will not function with equal efficiency relative to a given task, just as distinct keys usually cannot fit the same lock equally well.

The advantage of least entropy is a consequence of this varying capacity for work of a particular kind among the systems

of an ensemble. Clearly, by an appropriate contraction in state entropy the less capable systems will be removed, and therefore the ensemble will be more efficient as regards the particular kind of work. Some pure ensemble, containing only systems of the most capable kind, will be most efficient. However, such an ensemble will generally be capable of performing fewer types of work than one with greater diversity. For example, consider a box containing several types of nails, each of which is most suitable for some task. Appropriate reduction in the diversity of the box can increase its adaptedness, but at the expense of adaptability.

It is necessary to define the notion of type of work more clearly. From the point of view of thermodynamics capacity for work decreases with increasing entropy. According to Carnot's theorem, all reversible systems operating between the same two temperatures are equally efficient. The efficiency of irreversible processes is less than this, and depends on the details of path, on the particular values assumed by the system. Least state entropy differs from the purely thermodynamic principle since it is connected with the closeness with which an ensemble approximates any given path. It is a behavioral principle. Thus, type of work is work associated with a certain family of paths. Certain members of this family will allow more efficient utilization of energy, and therefore reduction in the state entropy may increase the efficiency of a system. This is true, in particular, because efficiency, or degree of reversibility, is more dependent on constraints which control the use of energy than on the quality of energy.

For example, biological systems convert high grade energy to lower grade energy with the production of thermal, mechanical, or chemical asymmetries. Certain of these asymmetries will be coupled to the reproduction process, or to the system's status in the matter cycle, and others will not. Thus least state entropy is important whether or not the diversity of a biological system is significant on a thermodynamic scale, since we are here dealing with the closeness with which the system achieves some given type of behavior, or produces some given pattern of asymmetries. Constraints, and the diversity of constraints, are more important in this respect than thermodynamic entropy, since these control the coupling of processes. Thus an appropriately constrained ensemble of high entropy may approximate a given behavioral pattern better than a less appropriately constrained ensemble of low entropy. In the long run asymmetries uncoupled to the reproduction process will not be maintained and will appear as heat. Ambiguities arising from transient asymmetries will be eliminated, and the most efficient system will be most efficient from the point of view of energy utilization, with no necessary reference to type of work or family of paths.

Contraction of entropy is a consequence of selection, since it is antithetical to the principle of maximum entropy, which is the condition for equilibrium in reversible processes, and to the principle of least entropy production, which is the condition for steady state in irreversible processes. Appropriate contraction in entropy produces an increase in adaptedness relative to a given environment. Thus least state entropy corresponds to specialization

of labor. However, specialization of labor may be associated with the evolution of more efficient adaptations, and not just with the reduction in variability of a given ensemble. Thus, as remarked previously, the efficiency of a system can increase without reduction in variability. This efficiency is related to the way in which the system's design is selected or restricted for a given task. I will call such restriction the internal specialization of the system, as opposed to external specialization, involving only reduction in variability. As adaptation increases internal specialization increases, although the converse is not necessarily true.

VI. Internal Specialization

The internal specialization of a compartment should be related to its diversity and inhomogeneity in terms of subcompartments--to its degree of differentiation. This increases as the heat of formation from subcompartments increases. However, we might also try to express differentiation in terms of the amount of selection required to describe the system given the types of subcompartments. The amount of selection, or information, equals some initial uncertainty minus some final uncertainty.

The final uncertainty is provided by the type entropy

$$\hat{\Gamma}(c_i^j) = - \sum_r f({}_i^j c^{j-1}_{\equiv r}) \log_2 f({}_i^j c^{j-1}_{\equiv r}) \qquad (13)$$

where $\Gamma(c_i^j)$ is the type entropy of compartment c_i^j and $f({}_i^j c^{j-1}_{\equiv r})$ is the frequency of subcompartments of type r. Types may fall into discrete classes or may be determined on the basis of overall

similarity analysis. In the latter case refinement of the analysis must not change the distribution of types in each class.

Type entropy reaches a maximum, $\hat{\Gamma}(c_i^j)_{max}$, when all frequencies are equal. The index of internal specialization, or degree of differentiation, is given by

$$\hat{\Gamma}_d(c_i^j) = \hat{\Gamma}(c_i^j)_{max} - \hat{\Gamma}(c_i^j) \tag{14}$$

where the maximum type entropy provides the initial uncertainty. The index, like the state entropy, is an extensive property, and therefore most conveniently defined per unit biomass. As such state entropy and internal specialization characterize compartments or levels of organization. However, the latter is sometimes expressed as a ratio

$$D_i^j = \frac{\hat{\Gamma}_d(c_i^j)}{\hat{\Gamma}(c_i^j)_{max}} \tag{15}$$

giving a value between zero and one.

The index of internal specialization represents the restriction on relative frequencies of different types of compartments, given the types of compartments in the system. It is important to distinguish this from redundancy, associated with restriction on the relative frequency of components (symbols, for example) which are processed by the system.

The constraining relationships underlying redundancy differ from those underlying internal specialization. Redundancy relationships are characterized by the fact that the operation of only some

of the parts is sufficient for the operation of the system. This is possible if the relationships involve repetition of components, complication of the pattern of connection of components, multiple distribution of operations, or other forms of parallelism. For example, see Winograd and Cowan (1963) for a discussion of how error correcting codes can be embodied in the interconnection pattern of networks. Redundancy changes relative frequencies of components in only an incidental way, and may in fact result in a decrease in the number of types.

Internal specialization relationships are characterized by the fact that the operation of many parts are necessary for the operation of the system, as in a series connection. Here the parts rely on one another, or are coadapted in the sense that they function in an environment of other parts. Such fitting relations become more intolerant as the internal specialization increases, since this amounts to an increase in the diversity and inhomogeneity of the internal environment.

Redundancy is associated with adaptability; internal specialization with adaptedness. Actually the two categories of relationship are not independent, since the redundant system must be associated with a coding apparatus.

Whether or not D_i^j is a satisfactory indication of internal specialization is a question that can only be decided on the basis of its usefulness. However, our intuitive picture of the complexity or internal specialization of biological systems is expressed by such indices. In the next two sections I will discuss the relation

between the state entropy of a system and the uncertainty of the environment; in the succeeding sections I will return to the relationship between state entropy and internal specialization. The particular indices discussed will play no essential role at present. However, the validity of the discussion can only be assessed through comparisons with biological nature, even if this is only in terms of an intuitive picture.

VII. Static Equilibrium

In this section I will attempt to show that the variability of a biological system tends to equal the variability of its environment.

> The state entropy of a biological system tends to equal the state entropy of its environment plus the noise entropy. The state entropy of a biological system can be smaller if this is compensated by entropy associated with equivalent configurations.

The system utilizes information about certain environmental events and not others. For example, the system may require information about certain macroscopic conditions, conditions such as temperature, salinity, pH, in order to adjust to these. The system is also subject to other events, events associated with Brownian motion, radiation damage, and so forth. The system must cope with such noise, but this does not involve any transmission of information. In general, biological systems contend with these various uncertainties by adjusting to them through adaptability mechanisms, blocking them with selective dissipation, or by tolerating a certain amount of damage. The systems which do this most efficiently, and which therefore have favorable survival curves, are the ones with least entropy

in both macroscopic and microscopic senses. Naturally, there are physical features of the objective environment, features which are more or less variable, which do not affect the system. Mechanisms for such interactions may not have evolved, or the system may have evolved in such a way that it can avoid or isolate itself from such interactions.

I will begin with a discussion based on Shannon's theorem ten, or what Ashby calls the law of requisite variety. Then I will consider the applicability of least state entropy. Actually this depends on the fact that an information processing system is characterized by a definite capacity even in the presence of noise. Finally, I will consider the physical and biological significance of the vaious terms.

In general

$$\Gamma[S^*(t),\ S_i^j(t+\tau_b)\,|\,\bar{S}_i^j(t)] \geq \Gamma[S^*(t)\,|\,\bar{S}_i^j(t)]. \tag{16}$$

In accordance with Shannon this can be expanded to give

$$\Gamma(S_i^j|\bar{S}_i^j) \geq \Gamma(S^*|\bar{S}_i^j) - \Gamma(S^*|\bar{S}_i^j,S_i^j) \tag{17}$$

where the dependence on time, unimportant according to the assumptions discussed in section IV, has been omitted for the sake of convenience. Actually, (17) follows directly from equation 5 (map b). The first term on the right hand side of the inequality expresses the uncertainty in the environmental state given the complementary or controlling state; this uncertainty would be reduced if there are definite relations between these states, relations of the type

expressed in maps a and c (equations 4 and 6). The second term represents information which is lost. This loss may be split into two terms

$$\Gamma(S^*|S) = \Gamma_I(S^*|S) + \Gamma_{II}(S^*|S) \tag{18}$$

where $S = (\bar{S}_i^j, S_i^j)$ and the symbolism expresses the fact that the sum can be viewed as describing the concatenation of a noiseless machine with a noisy communication channel. Accordingly, the first term represents the information loss associated with repetitions in the columns of the matrix corresponding to b. The second term represents information loss arising from noise processes implied by (12). Naturally, it is possible to construct matrices (with transition probabilities) for which the inequality in equation 17 holds.

In general

$$\Gamma(S^*, \bar{S}_i^j) = \Gamma(S^*) + \Gamma(\bar{S}_i^j|S^*) = \Gamma(\bar{S}_i^j) + \Gamma(S^*|\bar{S}_i^j). \tag{19}$$

Substituting for $\Gamma(S^*|\bar{S}_i^j)$ in (17),

$$\Gamma(S_i^j|\bar{S}_i^j) \geq \Gamma(S^*) + \Gamma(\bar{S}_i^j|S^*) - \Gamma(\bar{S}_i^j) - \Gamma_I(S^*|S) - \Gamma_{II}(S^*|S). \tag{20}$$

Rearranging,

$$\Gamma(S_i^j|\bar{S}_i^j) + \Gamma(\bar{S}_i^j) + \Gamma_I(S^*|S) + \Gamma_{II}(S^*|S) \geq \Gamma(S^*) + \Gamma(\bar{S}_i^j|S^*) \tag{21}$$

and

$$\Gamma(S) + \Gamma_I(S^*|S) + \Gamma_{II}(S^*|S) \geq \Gamma(S^*) + \Gamma(\bar{S}_i^j|S^*) \tag{22}$$

where

$$\Gamma(S) = \Gamma(S_i^j, \bar{S}_i^j) = \Gamma(S_i^j | \bar{S}_i^j) + \Gamma(\bar{S}_i^j). \tag{23}$$

Notice that

$$\Gamma(S) \leq \Gamma(S_i^j) + \Gamma(\bar{S}_i^j) \leq \sum_{i,j} \Gamma(S_i^j). \tag{24}$$

Therefore

$$\Gamma(S_i^j) \geq \Gamma(S^*) + \Gamma(\bar{S}_i^j | S^*) - \Gamma(\bar{S}_i^j) - \Gamma_I(S^* | S) - \Gamma_{II}(S^* | S) \tag{25}$$

which is essentially the requisite entropy principle. Here the states of interest are controlled in the face of an uncertain environment, assuming that the right hand side is small. In this case it is necessary to transmit information about the environment to the controlling compartments--the states of these compartments must be appropriately coordinated to the state of the environment. Accordingly $\Gamma(\bar{S}_i^j | S^*)$ represents noise entropy, or entropy associated with the operations of the system. However, there are no preferred compartments in biology--to a greater or lesser degree states of interest may control complementary states. For example, it may be important to control the physical condition of the DNA molecule--to maintain it in a homeostatic environment. The physical properties of the molecule may be quite certain, but the sequence of nucleotides quite uncertain. This uncertainty is used to control states at the population level, and ultimately to control the physiological environment of the molecule. Thus, we might as well interchange S_i^j and $\bar{S}_i^j$ in equation 16 and sum over all indices. This gives

$$\Gamma(S) + \Gamma_I(S^* | S) + \Gamma_{II}(S^* | S) \geq \Gamma(S^*) + \frac{1}{\sum_j i_j} \sum_{j,i} \Gamma(S_i^j | S^*) \tag{26}$$

in place of (22) where $\frac{1}{\sum_j i_j} \sum_{i,j} \Gamma(S_i^j|S^*)$ is now the noise entropy, and i_j is the number of compartments at level j. This can be split into two terms

$$\sum_{i,j} \Gamma(S_i^j|S^*) = \sum_{\substack{j,i \\ j<u}} \Gamma(S_i^j|S^*) + \sum_{\substack{j,i \\ j\geq u}} \Gamma(S_i^j|S^*) \tag{27}$$

where the first is associated with reliability, or component failure, and the second is associated with competition, i.e., with the fact that a biological system may have to cope with the uncertain behavior of other biological systems as well as with the external environment.

The first term is important for compartments at lower levels and the second for compartments at higher levels.

The left hand side of (26) represents the size of the ensemble of states associated with a biological system. Only certain states are consistent with the functions of such a system--for example, with growth in size or numbers, or just self-maintenance. Thus the ensemble size has an upper bound

$$\Gamma(S) + \Gamma_I(S^*|S) + \Gamma_{II}(S^*|S) \leq \Gamma(P) \tag{28}$$

where P is the set of permissible states. Usually the left hand side will be much smaller than $\Gamma(P)$. In fact, according to the least entropy principles it should be as small as possible; otherwise the system will be absorbed, or eaten, by other systems in the matter cycle. The left hand side takes on its smallest value when

$$\Gamma(S)+\Gamma_I(S^*|S)+\Gamma_{II}(S^*|S)\rightarrow\Gamma(S^*)+\frac{1}{\sum_j i_j}\{\sum_{\substack{j,i\\ j<u}}\Gamma(S_i^j|S^*)+\sum_{\substack{j,i\\ j\geq u}}\Gamma(S_i^j|S^*)\} \quad (29)$$

where we require that $\Gamma_{II}(S^*|S) \rightarrow 0$, since the undesirable loss of information cannot contribute to the regulation of any of the system states. According to the coding theorems of information theory this is possible, and the arrow can be replaced by an equality in the limit.

Combining (26) and (24),

$$\sum_{i,j}\Gamma(S_i^j)+\Gamma_I(S^*|S)+\Gamma_{II}(S^*|S)\geq\Gamma(S^*)+\frac{1}{\sum_j i_j}\{\sum_{\substack{j,i\\ j<u}}\Gamma(S_i^j|S^*)+\sum_{\substack{j,i\\ j\geq u}}\Gamma(S_i^j|S^*)\}. \quad (30)$$

According to least entropy the left hand side should again be as small as possible, since compartments are more efficient if the ensemble of states associated with them is smaller. In general, however, we cannot approach an equality, since the states of the compartments are not independent. For example, the sequence of nucleotides in the DNA molecule, quite uncertain of itself, provides information about the sequences in cells of the same or other organisms. As another example, the state of a highly controlled compartment is independent of the state of controlling compartments, at least over a certain range. However, the states of different controlling compartments of the same type are very likely to be influenced by each other or by the same environmental facts.

Some of these problems are avoided if we restrict ourselves to level structure. Here it is reasonable that the conditional relations will be unimportant. Information certainly passes between

levels of a biological system. The composition of a level may be determined by the composition of other levels--for example, the genes provide information about the composition of all levels. However, the possible states of different levels are quite independent--the sequence of nucleotides in the gene does not determine which of its possible states the cell, the organism, or the ecosystem is in. Accordingly

$$\sum_j \Gamma(S^j) + \Gamma_I(S^*|S) + \Gamma_{II}(S^*|S) \to \Gamma(S^*) + \frac{1}{\sum_j i_j} \left\{ \sum_{\substack{j,i \\ j<u}} \Gamma(s_i^j|S^*) + \sum_{\substack{j,i \\ j\geq u}} \Gamma(s_i^j|S^*) \right\} \quad (31)$$

where

$$\Gamma(S^j) = \sum_j \Gamma(s_1^j, \ldots, s_n^j). \quad (32)$$

This is the state entropy characteristic of level j. $\Gamma(S^j)$ may be taken as the average of the entropies associated with different types of compartments at the level, weighted by their fraction of total biomass. This is possible if types can be chosen in such a way that they are reasonably independent; otherwise conditional relations among types must be taken into account.

A compartment, such as c_i^j, can be regulated to the extent that environmental uncertainty and noise are removed by $\Gamma(\bar{s}_i^j)$ or selectively destroyed by $\Gamma_I(S^*|S)$. This is also true for levels. However, the contribution from selective loss of information must be restricted; otherwise the system will be incapable of utilizing essential features of the environment.

It is evident that the ensemble of system states can be smaller if the noise entropy is smaller, since the matching of environmental and complementary states can be more appropriate in this case. This can be achieved by isolating components, or through communication processes, involving feedback or prediction, associated with maps of type a and c (equations 4 and 6). Reduction in $\sum_{\substack{j,i \\ j \geq u}} \Gamma(S_i^j | S^*)$ indicates a high degree of cooperation or coalition within the system, and as before systems which achieve this will have an advantage.

The function of information loss is not a clear cut matter. Nonselective loss of information is associated with noise entropy, whether or not this is inherent in the system. However, such loss of information about the environment is necessarily concomitant to evolution. This is implied by the notion of variation and natural selection, and in fact the non-unique relation of system and environment can be regarded as expressing the mutability of the system. Such information loss, desirable from the point of view of long term regulation, will appear as state entropy of the system or certain of its compartments, and should be associated with the correction capacity of the system. Increase in competition also increases the capacity or the information loss, but it is not always clear which.

The terms appearing in equations 29 to 31 represent various processes taking place within a biological system. The right hand sides represent macroscopic uncertainty of the environment as well as pertinent microscopic uncertainty, where environmental events are

those over which the system exerts relatively little control. $\Gamma(S)$, the $\Gamma(S_i^j)$, or the $\Gamma(S^j)$ represent the macroscopic uncertainty of system states, compartment states, or levels. When the system is examined these will include a contribution from $\Gamma_{II}(S^*|S)$. It is somewhat more difficult to interpret the $\Gamma_I(S^*|S)$ term, and we will return to it in the next section. However, in some cases it is associated with the microscopic uncertainty produced by the system, or the ensemble of states identical from the macroscopic point of view. From the standpoint of efficiency this ensemble should also be as small as possible.

We can symbolize the above interpretations

$$\Gamma(\text{system}) \rightarrow \Gamma(\text{environment}) \tag{33}$$

where Γ(environment) is the noise entropy and state entropy of the environment and Γ(system) is the adaptability of the system.

VIII. Further Discussion; Network Analogies; Vector Representation of Biological Organization

The symmetry between system and environment expresses a tendency which might be expected in the course of evolution, not any exact or rigorous condition. In this section I will put the principle in perspective by considering some of the assumptions with which it is associated.

In the limiting case equation 29 (or 31) is reminiscent of the static equilibrium of forces around a point: equality of action and reaction, Kirchoff's laws, conservation of mass in hydraulic

mass flow, and so forth. For example, $\Gamma(S^*)$ can be analogized to an applied force, $\Gamma(\bar{S}_i^j)$ to an elastic compliance, $\Gamma(S^j)$ to an inertial element, and $\Gamma(S^*|S)$ to a dissipative element. As another example, $\Gamma(S^*)$ is analogous to the mass flowing into a region in hydraulic mass flow. This must equal the sum of the mass leaving the region, the mass increase in the region, the mass loss due to leakage, minus sources of mass which are regarded as internal. These are analogous to $\Gamma(\bar{S}_i^j)$, $\Gamma(S^j)$, $\Gamma(S^*|S)$, and $\frac{1}{\sum_j i_j} \sum_{j,i} \Gamma(S_i^j|S^*)$, respectively.

Principles of static equilibrium always tie the elements of a network together. In the case of an information network, static equilibrium expresses the notion that impinging entropy will be filtered out, siphoned off by correction channels, or absorbed in the region of interest. If one region of the net becomes cool, in terms of variability, some other region of the net must become warmer. It is important, however, that the regions of high and low variability might be at different levels of biological organization.

The correctness of these analogies depends on the correctness of the least entropy assumptions. Least state entropy is achieved by contracting an ensemble of systems, through elimination of the least efficient, or by contracting the possible states of a single system. In order to approach an equality the contraction must be appropriate. This is possible if the operations of the system impress the appropriate spatial and temporal organization on the pattern of environmental states. As previously discussed such coding involves parallelisms or redundancies of various kinds. According to the least entropy assumption states in excess of the minimum reduce the

efficiency of the system, especially if it is internally specialized. However, as the minimum is approached the number of operations which the system must perform increases. This might also reduce the efficiency of the system, limiting the contraction in entropy or the number of operations which can be associated with error correction. In the latter cases controlled states would absorb a certain amount of noise.

The information loss term represents processes which block out environmental states. This is achieved through dissipative processes which free the system from certain initial conditions. For example, according to Schrödinger (1944) biological systems must be large in order to be independent of random fluctuations in the environment. Here what are fluctuations in one system will not appear as fluctuations in any essential variables of another system. Many protective mechanisms, such as rigid structures, play a similar role. The processes of perception, of singling out the essential features of the environment, must also involve some selective dissipation, although selective interaction with the environment is also important. Computation processes, such as the encoding and decoding operations underlying many error correction mechanisms, also require controlled loss of information. In each of these examples initial details are absorbed into the ensemble of equivalent states. The absorbtion process is less dissipative if the ensemble of equivalent states is smaller, but in this case the possibility for error increases. (Of course the organization of the system arises from selective dissipation, from the particular pathways by which heat is exported to the

environment, but here we are interested in the control of these pathways. This is the difference between the composition of a system and its variability).

It should also be emphasized that it is the system's uncertainty about the environment, not the biologist's which is important. There may be correlations in the environment which are not used by the system. Furthermore, it is a problem to determine which conditions of the environment are really important. Certainly it would be difficult to determine the uncertainty of the environment on the basis of what is pertinent to the system--in fact, this may be under some control. The system may interact selectively with certain features of the environment or it may be able to select the environment in which it operates (niche selection). It is probably convenient to include such specificity and avoidance reactions in the information loss term.

Statistical and hierarchical aspects of biological organization can be represented in the form of a vector model, as illustrated in figure 1. Γ(environment) is represented on the abscissa and Γ(system) on the ordinate. Γ(system) can be described in terms of component vectors--for example, the $\Gamma(S^j)$ and the dissipation term, where the latter is associated with the lowest level. Γ(environment) is also divided into (equal) components, each associated with one of the system vectors. These represent the fraction of environmental uncertainty which each level might be expected to handle, all things being equal. The individual vector sums may form any angle with the coordinate axes, but, according to static equilibrium, the total sum

should always form a diagonal. Vector sums pointing above the diagonal line are associated with controlling levels; sums pointing below the line are associated with controlled levels.

If types of compartments are taken into account the components of the environment vector can be weighted according to the fraction of biomass associated with the type. In what follows I will assume that the dissipation term does not change too fast in the course of evolution--in any case I will subtract this term from the environment vector and consider only the $\Gamma(S)$ part of adaptability.

The main significance of the static equilibrium relationship is that it imposes a certain total uncertainty on a biological system--the distribution of this uncertainty to the compartments must be consistent with this total. The covariance of individual sums in the vector model is at best an idealization, but the tendency of biological systems to fulfill this condition should help to account for some of the tendencies exhibited in the course of evolution. The quantitative correctness of the principle, the extent to which the limiting values are reached, is not as important as whether the total uncertainty can be treated as an approximately conserved quantity. The validity of this hypothesis, as well as the validity of related assumptions about coding, reliability, information loss, absorbed variability, and so forth can only be determined by the constructing models of biological organization.

IX. Allocation of the Entropies

There is evidence, drawn from computer experiments, that the

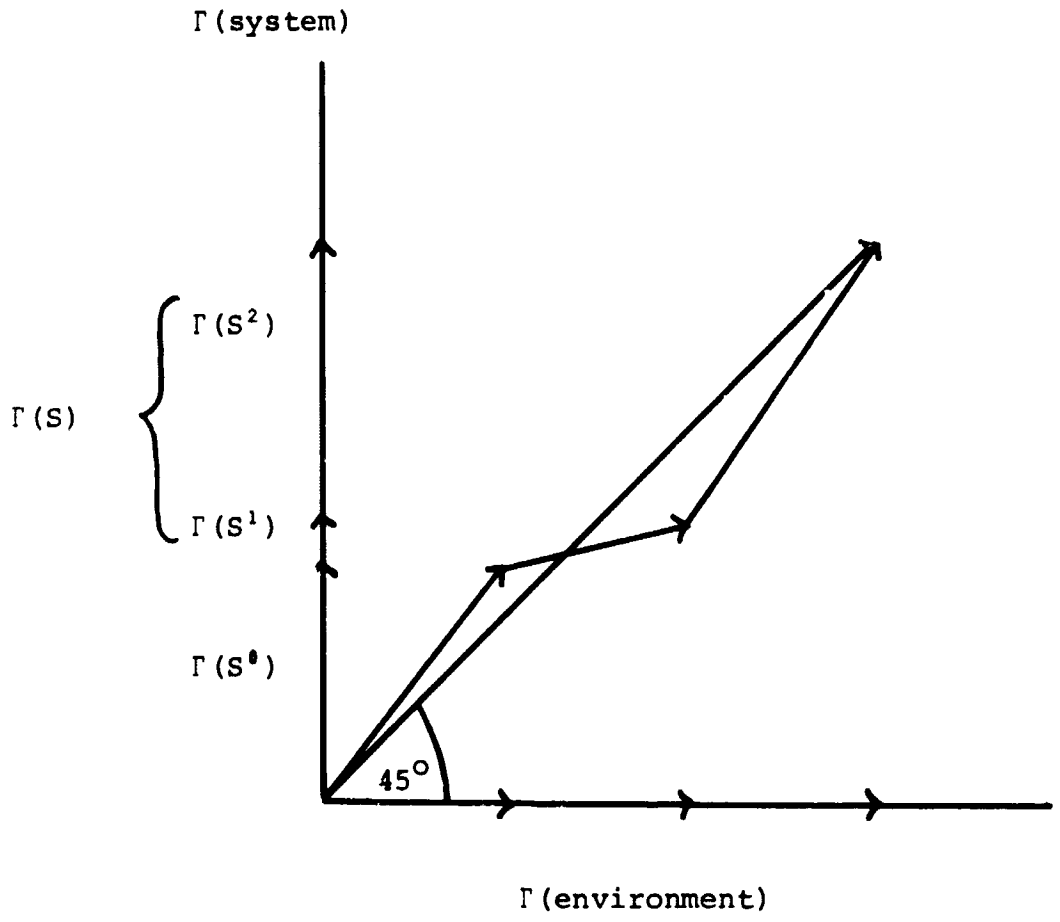


Fig. 1. Vector diagram with two controlling levels and one controlled level. $\Gamma(S^0) = \Gamma(S^*|S)$.

efficiency of the ecosystem increases in the course of evolution, where efficiency is the ratio of actual to maximum utilization of energy and materials (Conrad, 1969). This depends on adaptedness to specific environments, and on adaptability, where the latter amounts to the system's adaptedness relative to an ensemble of possible environments,or to the environment in the long run. The adaptability of a system, its statistical or control characteristics, might expand or contract within the framework of certain essential constraints. For example, changes in the variability of the gene pool might depend on minor physiological changes. Changes in behavioral plasticity might also take place relatively fast on an evolutionary time scale, without major changes in the differentiation of the organism or the nervous system. In contrast, the development of new types of adaptations, such as new reproductive or behavioral mechanisms, requires longer periods of time.

The actual efficiency depends on the intrinsic and extrinsic relations of the system, relations hard to analyze in general. This efficiency changes as the adaptability of different compartments changes. It is plausible that the restrictions on relations--the internal specialization--play an important role in this process. I will assume that this is so, and that change in efficiency can be described to some extent without reference to detailed relations. Accordingly

$$U = U\ (\Gamma_1, \ldots \Gamma_n;\ D^1, \ldots D^n;\ D^{n+1}) \tag{34}$$

where U is the net return in efficiency, Γ_i represents $\Gamma(S^i)$, the

adaptability of level i, D^i is the internal specialization ratio characteristic of level i, and D^{n+1} is a factor associated with the physical environment. Here we are ignoring the compartmental structure of biological organization and are characterizing levels as a whole. The notation would otherwise be somewhat more complicated.

Adaptabilities of different compartments do not interact, in the sense that the adaptability of one should not affect the adaptabilities of others. Furthermore, adaptability may change without significant changes in internal specialization. Thus

$$U = \sum_i U_i \ (\Gamma_i;\ D^1,\ldots,D^n;\ D^{n+1}) \tag{35}$$

where U_i is the net gain associated with level i. We will suppose that the internal specializations are given, and that the uncertainty of the environment is also a given fact. What is of interest are the factors which determine the allocation of adaptability to different levels of biological organization.

Net gain can be split into two terms

$$U_i = G_i - L_i \tag{36}$$

where G_i is a gain function and L_i is a loss function. This splitting is not necessary, but it is convenient to distinguish gain, associated with the requirements of adaptability from loss in adaptedness concomitant to this adaptability.

Gain in efficiency follows from the fact that adaptability must approximate the uncertainty of the environment. Thus U must

be maximized subject to the constraint

$$\Gamma - \sum_i \Gamma_i = 0 \qquad (37)$$

where $\Gamma = \Gamma(\text{environment}) - \Gamma(S^*|S)$ and $\Gamma_i \geq 0$ for all i. The system will be perturbed or injured if the adaptability is less than the required amount. This will reduce the efficiency of the system, since its relative capacity to utilize the environment will be decreased until the damaged parts are repaired or grow back. The gain in efficiency could be expressed in terms of the constraint (37), except that the gain deriving from any particular compartment may be associated with diminishing returns. For example, it may be difficult to couple the variability of some compartment to the control of certain processes; or delays and other inefficiencies arising from the variability of a compartment might not be compatible with the operation of the system. In the absence of some such non-linearity, either in the gain or loss function, all of the adaptability will concentrate in one of the compartments.

The system also loses efficiency as adaptability increases. This is the converse of the least entropy principle, according to which the efficiency of a system, in any given environment, increases with appropriate contraction in the state entropy. Usually the efficiency will not increase, since the chances are that the most efficient system will be eliminated. Likewise, efficiency will fall off with expansion of the state entropy, assuming that the new variations are not more efficient than the original system. The

possibility of more efficient variations is important from the point of view of evolution; from the point of view of biological organization, however, the rate at which efficiency falls off is important.

The interference between efficiency and adaptability is influenced by internal specialization. As suggested by equation (35), the adaptability of a compartment has a complementary relationship to the internal specialization of certain other compartments. This will be discussed in the next section.

X. Complementary Relations

Loss in efficiency depends on the internal specialization characteristic of a level, and on the environment. The first of these factors has to do with whether the system is well formed, in the sense that its parts must be related in a way which is functional in any conceivable environment. Rearrangements of parts are more likely to interfere with such relations as the system becomes more differentiated, or as the relations among parts become more restrictive. The system also operates in an environment which is more or less homogeneous or diverse. Variability is more likely to reduce the adaptedness of a system in a differentiated environment, since the relationship between compartment and environment is usually more specific in this case. For example, a cell may be highly differentiated internally, in which case variability will be expensive. The cell may also function in an environment (organism or society of cells) which is highly differentiated. It must be

coadapted to the cells of this society, and this will also increase the cost of variability.

The environment includes the external, physical environment. Here the restrictiveness of relations is determined by the availability of energy and materials. In part this depends on the thermodynamic asymmetry (or specialization) of the environment. For example, the thermodynamic asymmetry decreases at higher trophic levels, since much of the initial energy has already been degraded. As a consequence, utilization of energy at higher trophic levels often involves more differentiated organs. The availability of energy and materials is also affected by purely physical features of the environment, features which may themselves require more or less specialized energy transducers, but I will not discuss this at present.

There are prominent exceptions to these generalizations. These are the special organs of variability--for example, the genetic system, the immunity system, the central nervous system. These organs have a more or less universal property, since they may be tailored or programmed for different modes of behavior. The essence of this property is the isolation of certain crucial constraints from certain adjustable constraints. In this case variability does not disturb the internal structure of the organ as much as usual, but it may still disturb the relations between system and environment. However, the complementarity of internal specialization and adaptability holds in a broad sense, since the system will be

particularly sensitive to the conditions affecting the maintenance and construction of essential constraints. This increases the cost of variability at higher or lower levels of organization. For example, the operation of the genetic readout machinery requires a highly controlled cellular environment; the operations of the central nervous system require some highly differentiated cells.

Really effective redundancy mechanisms also require a high degree of internal specialization at some level, providing for encoding and decoding operations. Thus, an increase in internal specialization may often be associated with an increase in stability or adaptability. For example, the stability of a foodweb often increases with an increase in internal specialization relative to the species composition of the ecosystem (Margalef, 1958). This is possible because the internal specialization provides a basis for redundancy in the processing of materials, or control over the possible pathways of energy in the system (see Conrad, 1969).

It is important that all compartments are to some extent described by the genome--certainly the proteins of the cell are so described, and through these the cell and the organism. The characteristics of organisms which produce coadaptation at the social and higher population levels are also reflected in the genome description, in the sense that phenotypic correlations must be associated with genotypic correlations. Thus, loss in efficiency associated with the variability of the gene pool depends in some way on the internal specialization of the compartments described. It does not depend on the internal specialization of the gene pool

itself, since the genome does not describe itself; the genome does describe the readout machinery, but the probability that this will be affected by variability should be fairly independent of the nature of the genome.

Gene pool variability favors the continuity of lineages. As such it renders the ecosystem more independent of the environment apropos its composition in terms of types. This is a kind of statistical stability. The internal specialization underlying foodweb stability reduces oscillations of the ecosystem by reducing the competition term. As such it renders the ecosystem more independent of the environment apropos the frequency of types. This is a kind of mechanical stability. Evidently there will be some interference between foodweb stability and the adaptability of the gene pool, since genetic variability must be consistent with correlations at the top level of the ecosystem. Accordingly, the genetic system may itself develop homeostatic features in order to conserve these correlations. Biological systems often develop latent mechanisms of variability--dominance, suppression, inversion, and so forth--to evade the immediate consequences of this interference.

XI. Models of Biological Organization

In this section I would like to illustrate the preceding discussion with a definite model, based on the simplest assumptions.

Assume that the gain function exhibits diminishing returns and that this can be expressed as

$$G_i = 1 - e^{-\alpha_i \Gamma_i} \tag{38}$$

where $\alpha_i > 0$ for all i. Also, for simplicity, assume that the loss function is linear

$$L_i = \sum_j d_{ij} \Gamma_i \tag{39}$$

where we define

$$d_{ij} = f_{ij} (D^j). \tag{40}$$

The f_{ij} are (unknown) functions relating the (given) internal specialization ratio of level j to the adaptability of level i.

Evidently we must maximize

$$U = \sum_i (1 - e^{-\alpha_i \Gamma_i} - \sum_j d_{ij} \Gamma_i) \tag{41}$$

subject to the constraint

$$\sum_i \Gamma_i = 1, \ \Gamma_i \geq 0 \tag{42}$$

where Γ has been set equal to 1 for convenience. Note that

$$U_i' = \alpha_i e^{-\alpha_i \Gamma_i} - \sum_j d_{ij} \tag{43}$$

and

$$U_i'' = - \alpha_i^2 e^{-\alpha_i \Gamma_i} \leq 0 . \tag{44}$$

Thus all the U_i are concave downwards. In this case efficiency is maximized if the system shifts from a curve U_j to a curve U_i only

when the slopes of these two curves are the same. Accordingly,

$$U_i'(\tilde{\Gamma}_i) = \lambda \iff \Gamma_i > 0 \tag{45}$$

where λ is the slope and $\tilde{\Gamma}_i$ is the value of Γ_i when U is maximized. This shift will only occur if the slope of U_i at point zero is greater than λ, and will certainly occur if it is. Thus

$$U_i'(0) > \lambda \iff \tilde{\Gamma}_i > 0. \tag{46}$$

Combining (43) and (45)

$$\tilde{\Gamma}_i = -\frac{1}{\alpha_i} \ln \left(\frac{\lambda+\sum_j d_{ij}}{\alpha_i}\right) \tag{47}$$

where $\tilde{\Gamma}_i > 0$. Together with the constraint (42) this gives

$$-\sum_{\substack{i=1 \\ \tilde{\Gamma}_i>0}}^{n} \frac{1}{\alpha_i} \ln \left(\frac{\lambda+\sum_j d_{ij}}{\alpha_i}\right) = 1. \tag{48}$$

According to (46) the condition $\tilde{\Gamma}_i > 0$ implies that

$$U_i'(0) = \alpha_i - \Sigma_j d_{ij} > \lambda \tag{49}$$

and therefore $\tilde{\Gamma}_i = 0$ if the sum (48) is greater than one when λ is taken as $U_i'(0)$.

The values of λ and $\tilde{\Gamma}_i$ are determined by the values of the α_i and the d_{ij}. The latter can be expressed in a matrix

$$\begin{pmatrix} d_{11} & \cdots & d_{1(n+1)} \\ \vdots & & \vdots \\ d_{n1} & \cdots & d_{n(n+1)} \end{pmatrix} \tag{50}$$

where the choice of entries amounts to particular assumptions about biological organization. In the present discussion we will treat the organism (n=4) as the top level and will view the rest of the ecosystem as well as energy sources and other physical factors as the environment, associated with n+1. Thus $d_{n(n+1)}$ must reflect the availability of energy and materials.

Note that increasing values of d_{ij} will decrease the maximum value of U, the net return in efficiency, and an increase in the number of levels will have the opposite effect. From the point of view of overall efficiency the cost of developing or amplifying another level may be offset by this fact. When level i is absent we shall set $d_{ii} = \infty$ and $d_{ij} = d_{ji} = 0$ for all j. In this case adaptability cannot be allocated to the level.

We shall make the following assumptions, in rough agreement with the previous section.

1. Rearrangements of compartments are usually not affected by internal specialization of compartments at lower levels, and are affected most by the internal specialization characteristic of their own level and the immediately higher level. Thus

$$d_{ij} \begin{cases} > 0, \ j=i \text{ or } i+k \\ = 0 \text{ otherwise} \end{cases} \tag{51}$$

where k is the smallest integer for which $d_{(i+k)\,(i+k)} \neq \infty$ and we are ignoring the contribution of higher levels.

2. It is useful to distinguish developmental or growth adaptability from other forms of physiological adaptability which allow

the organism to adopt different modes of behavior. Organs (or levels) with a universal property are an extreme example of this. Here equation 51 is replaced by

$$d_{ij} \begin{cases} > 0, \; j=i+1, \; i+2 \\ = 0 \text{ otherwise} \end{cases} \tag{52}$$

and

$$d_{ji} > 0, \; j = i+1 \tag{53}$$

where i is the level. $d_{ii} = 0$, since rearrangements do not affect the organ itself, but this is compensated by the fact that the adaptability of higher levels is restricted (equation 53). Actually, differentiation of organ structure would also increase the restrictions on some compartments at the cellular level. The universal-like organ, as a form of physiological variability, is subject to the same environmental influences as variability at the organism level (equation 52, j=i+2); such variability is also restricted by the fact that it must be consistent with the internal operations of the organism (equation 52, j=i+1), although this factor may not be as important.

3. In the case of the genome (at level 1)

$$d_{ij} > 0, \; j > 1 \; . \tag{54}$$

These probably become less important as j increases, but they can never be ignored because of the mapping between genome and other levels. $d_{11} = 0$ since the genetic system has a universal-like property

Consider the coefficient matrices for systems with two levels (gene and cell), three levels (gene, cell, and organism), and four levels (gene, cell, universal organ, organism), called system I, II and III, respectively. For the sake of a numerical example, take all coefficients equal to .5, and α_i equal to 2 for all levels. The matrices and corresponding vector diagrams are given in figure 2. Notice that adaptability is mostly at the population (genetic) level in system I, mostly at the organismic level in system II, and mostly at the organ level in system III.

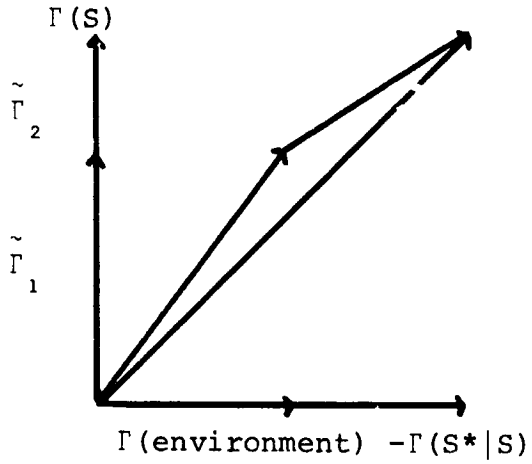
The above discussion shows how models of biological organization, embodying definite assumptions, can be constructed within the present theoretical framework. Certainly the present assumptions are overly simple from the standpoint of biology. I have not considered the $\Gamma(S^*|S)$ part of adaptability; α_i may be smaller for certain compartments, especially special organs of adaptability; the constraint (42) is probably not so exact, and the problems of approaching the ideal coding have not been considered; the particular assumptions embodied in equations 51 to 54 are naive and the numerical values are arbitrary; the compartmental character of the problem has really been ignored. Nevertheless, the model touches on some important processes underlying biological organization, and despite its artificiality, it is worth silhouetting it against the biological background.

XII. Characteristic Features of Biological Organization

The biological world contains three main life plans, or kingdoms; the protista, the plants, and the animals.

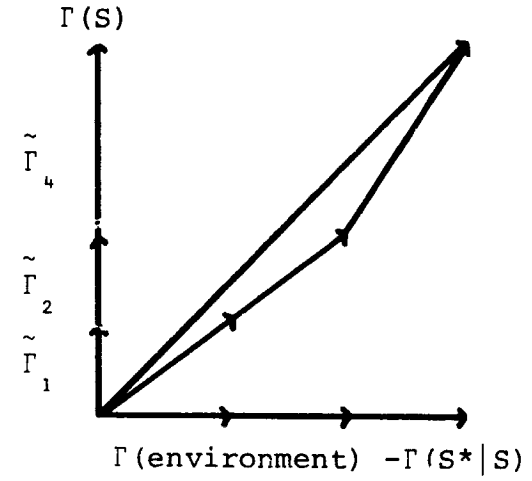
$$\begin{pmatrix} 0 & d_{12} & 0 & 0 & d_{15} \\ d_{21} & d_{22} & 0 & 0 & d_{25} \\ 0 & 0 & \infty & 0 & 0 \\ 0 & 0 & 0 & \infty & 0 \end{pmatrix}$$

I



$$\begin{pmatrix} 0 & d_{12} & 0 & d_{14} & d_{15} \\ d_{21} & d_{22} & 0 & d_{24} & 0 \\ 0 & 0 & \infty & 0 & 0 \\ 0 & 0 & 0 & d_{44} & d_{45} \end{pmatrix}$$

II



$$\begin{pmatrix} 0 & d_{12} & d_{13} & d_{14} & d_{15} \\ d_{21} & d_{22} & d_{23} & 0 & 0 \\ 0 & 0 & 0 & d_{34} & d_{35} \\ 0 & 0 & d_{43} & d_{44} & d_{45} \end{pmatrix}$$

III

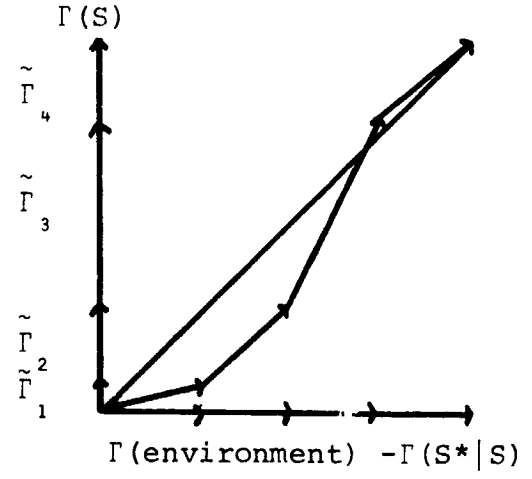


Fig. 2. Coefficient matrices and corresponding vector diagrams. The coefficient matrices are based on assumptions (52) to (55). System I is a unicellular organism, system II a multicellular organism, and system I a multicellular organism with a developed organ level. $\tilde{\Gamma}_1$ is associated with the gene (population) level, $\tilde{\Gamma}_2$ with the cell level, $\tilde{\Gamma}_3$ with the organ level, and $\tilde{\Gamma}_4$ with the (multicellular) organism level.

The protista are characterized by two important levels of organization. The first is the organism, which is a single cell, and the second is the population. As an example, consider the bacteria. The bacterial cell is capable of exhibiting physiological adaptability--it may, for example, possess a number of inducible enzymes. The bacterial population is also adaptable, as is evident from one of the standard methods of microbiology: the method of culturing bacteria. When the appropriate environment presents itself a particular bacterial type will be brought forth. Much of this diversity can be attributed to short generation time along with haploidy, although there may be a certain amount of cytoplasmic lag associated with multiple nucleii. Diversity also arises from the ability of bacteria to exchange genetic material through conjugation, transduction, and, perhaps, transformation in natural circumstances. This genetic interchange could occur in the context of hybrid complexes, allowing for the maintenance of types not adapted to the present environment. On the other hand, if an especially favorable adaptation is hit upon it could always be preserved by resorting to agamy. Inbreeding, agamy, and periodic mutation (usually conferring an advantage on the larger, original population, and therefore lowering the equilibrium proportion of mutants) damp unnecessary diversity, allowing for increased efficiency. In fact, in a narrow environment superfluous machinery, such as an unneeded inducible enzyme, puts a strain at a definite disadvantage, indicating that the requirements of least entropy may be very

exacting. In some situations a spore form may be adopted, thus blocking or avoiding an unfavorable environment.

The above picture, as regards the significance of sexual behavior, is not definitely established, although Ravin (1960) has presented strong arguments in its favor. Even if sexual mechanisms are not so important at the present time, they may have played an important role in the original processes of bacterial speciation. The basic relationships, in the case of the other lower forms, are similar, although the details differ greatly. For example, protozoa range from inbreeders and asexual diploids to outbreeders and asexual haploids (Sonneborn, 1957). The first group, with specific adaptation, may have a short term advantage, although this advantage can persist for a long time in a constant environment. It is interesting that asexual diploids possess a great deal of physiological adaptability due to the fact that multiple gene loci can respond differently to different circumstances. The second group, the outbreeders and asexual haploids, possess a great deal of evolutionary adaptability, but with loss of high adaptedness. Haploid asexuals may, like bacteria, multiply rapidly and depend upon mutation. Similar examples could be drawn from many other of the protista. What is important is the fact that in the simplest forms there are two component vectors to which the variability is allocated.

The higher plants exhibit a different pattern. Component vectors include the cell and the population, and also the (developing) organism. Plant cell types fall into definite categories. The

physiological adaptability of the various types is probably less than what can be found among the bacteria, at least while they are in the environment of the organism and after differentiation. However, as organisms, plants are remarkably adaptable. This is associated with their relatively simple morphology, which permits rearrangements, both in a developmental and comparative sense, to produce many different forms. This developmental plasticity, presumably controlled by quantitative alternations in a few growth hormones, allows the plant to accommodate itself to different environments, as well as to variations in a single environment. Developmental plasticity is consistent with reproductive plasticity, since new genetic information can be incorporated into the system without necessarily producing lethal results. Plants are capable of participating in extensive hybrid complexes, although there are mechanisms for preserving adaptations, such as ring chromosomes and agamy. In some cases, facultative apomixis makes the rapid colonization of a new environment possible by genetically similar individuals, with a later burst of variability due to hybridization. Adaptations can also be maintained by extensive gene flow, since this is the converse of the isolation conditions which favor speciation. In some plants the most apparent organs, flowers and fruits, are coupled to these breeding systems. It is also worth noting the increasing protection for the young embryo in the higher, more constrained of the plant forms. This is a clear parallel to the situation in the animal kingdom.

Finally, consider higher animals. The component vectors are the same as with plants, except that the society (of organisms) is often interesting. The animal organism, like the plants discussed above, is a society of cells. This makes possible greater specialization at the cellular level, and therefore greater efficiency. However, there are more histological types among animals than among plants, although the number of types and their adaptability is definitely limited. The greater differentiation of animals is associated with the fact that they belong to higher trophic levels. From the thermodynamic point of view the environment of a trophic level becomes less specialized--hence more difficult--as the height of the trophic level increases. The differentiation of higher animals is not incompatible with rearrangements in a comparative sense, but it precludes the developmental plasticity characteristic of plants. For example, in mammalian species there are many possible arrangements of veins, fewer of arteries, and still fewer of nerves and muscles. However, the skeletal system is much more definite in pattern, and all in all the possibilities for ontogenetic rearrangements are limited. This lack of developmental plasticity in turn precludes the degree of genetic interchange possible in the plant and microbial worlds, for variety entering a complex and highly differentiated structure is not likely to produce a viable result. In fact, this is attested to by the applicability of the biological species concept to, say, mammalian populations.

Thus, the cell, the developing organism, and the population cannot provide the required adaptability in higher animals. As a consequence special organs and organ systems must develop. For example, the nervous and neuromuscular systems make possible behavioral adaptability; in turn, this extends the possibilities for motion, for social organization, and for specialization and homeostatic action at a new level. The other main system of adaptability is the reticuleondothelial system, the defense system of the body. The antibody, associated with this system, is representative of an ensemble of molecules, whether produced by an instructive or selective mechanism--just as the genetic molecule is representative of an ensemble of molecules. This is a clear instance of the entropy requirement of a homeostatic function. It might be remarked that systems with such high variability as the nervous or immune system are peculiarly subject to turning upon themselves, as in autoimmune disease. Indeed, adaptability is always associated with disease, if the latter is broadly conceived in terms of loss in adaptedness.

In sum, simpler forms can be variable at the cellular and population levels. Higher plants are constrained at the cellular level, but compensate for this by variability at the (developing) organism and population levels. The higher animals are constrained at the cellular, organism, and populations levels. Variability must appear elsewhere, in special organs and in social organization. In general, increased specialization of one compartment of a

biological system must be compensated by increased adaptability of some other compartment. This follows because specialization is contingent upon the maintenance of constant conditions. As the internal specialization of subcompartments increases the cost of adaptability becomes prohibitive, and a new level of organization must appear if the increase is to continue. The appearance of this new level may open the possibility for novel constraints, for internal specialization at the higher level, and therefore for the more efficient exploitation of the environment.

Characteristic features of biological organization appear not for the sake of preserving any preferred entity of the biological world, but because they confer a preferred status in the matter cycle.

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