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BIFURCATIONS AND BIOLOGICAL OBSERVABLES

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INTRODUCTION

It is a truism that biological systems are complex. It has further come to be regarded as axiomatic that complex systems in general are "counter-intuitive". To set the stage for the subsequent discussion, it will be helpful to study these two propositions a bit further, and establish some relationships between them.

The term "complexity" is almost as hard to define as is life itself. Many approaches to complexity attempt to treat it as if it were an intrinsic property of a system, or class of systems, related somehow to entropy or "information". These approaches seek to obtain a single quantitative measure of complexity, in terms of the number of elements, interactions or operations required to characterize some aspect of system behavior. I would rather suggest that complexity is not an intrinsic property of a system; it must also reflect something about the manner in which we, as observers, can interact with the system.

Roughly, then, I would suggest that complexity is a property of system descriptions rather than of systems themselves. Indeed, we may say that a system *appears* complex when it is possible to generate many apparently independent descriptions of its behaviors. Each such independent description must arise out of a different process for observing the system, and hence out of a distinct available mechanism for us to interact with the system. Thus, a stone usually appears simpler than an organism, because we have only a few ways to interact with the stone, and many ways to interact with the organism. As we multiply our capabilities for interaction with the stone, its complexity grows; as we narrow our capability to interact with an organism, its complexity diminishes. Thus, complexity appears as a *contingent* rather than as an intrinsic property, and ultimately reflects interactive capabilities expressed in observation or measurement. It is these capabilities which provide the elements for corresponding system descriptions.

With this as background, let us consider what is meant by the proposition that complex systems are "counter-intuitive". Roughly, such a proposition connotes the

absence of an expected implication between two or more aspects of system behavior. If each such behavior arises from a particular mode of interaction or observation, and generates a corresponding system description, then the assertion of “counter-intuitive” behavior implies a logical independence between these modes of description. Let us be more precise about this: imagine a class K of systems, each of which can be described in two ways. Suppose that a body of experience exists which indicates that in some available subclass $K' \subset K$, one of these descriptions implies something about the other. We then come to expect that such an implication will hold for every system in K ; such an expectation provides the intuitive basis for relating the two descriptions. However, as soon as we encounter a system not in K' , the implication relation breaks down and we can say that such a system behaves in a “counter-intuitive” manner.

Such a breakdown of an expected implication between modes of system description is what we shall call a *bifurcation*. In general, a bifurcation indicates a situation in which distinct modes of system description are logically independent; i.e. in which properties of one description do not imply corresponding properties of the second. As will be seen, this usage subsumes the traditional mathematical definition, but substantially extends its scope. In general terms, a bifurcation manifests a situation in which the incompleteness of a given mode of system description becomes manifest, and hence must be supplemented or replaced by another. In the study of natural systems, such as biological organisms, the fundamental problems all ultimately concern the inter-relationships of different modes of description, and for this purpose the notion of bifurcation, or the absence of bifurcation, becomes a crucial tool. In the sections which follow, we wish to explore some of the ramifications of such ideas, treating bifurcation phenomena in the context of natural systems, and arising out of the comparison of differing modes of description of such systems.

SYSTEM OBSERVATION AND DESCRIPTION

In the preceding section, we suggested that each mode of description of a system arises from a corresponding behavior or interaction of the system which we can observe; conversely, each mode of observing a system generates a system description. In the present section, we shall develop some general properties of the relation between system interactions (observations) and the descriptions to which they give rise.

The basic unit of system description, and of system measurement, is a single observable. Intuitively, an observable of a system is a quantity which can induce dynamics in some appropriate meter; i.e. in some other system with which the given one can interact. A system can be regarded, at least in part, as simply a collection of observables; i.e. as a family of capabilities to induce dynamics in other systems.

A closely related concept is that of *state*. For present purposes, it is sufficient to regard a state s of a system S as connoting the specific dynamics which S can induce

in any particular meter at a specific instant of time. That dynamics, or its corresponding attractor, or some parameter value associated with that attractor, represents the *value* of the observable in question, evaluated on the state s .

Modern physics is dominated by the proposition that all “physically real” events involve observables evaluated on states. Furthermore, it is usually supposed that it suffices to consider observables which take their values in real numbers; i.e. the attractor states of all meters can be effectively parameterized by real numbers. Thus for present purposes, an observable is simply a mapping $f : S \rightarrow \mathbb{R}$ from states to real numbers. The image $f(S)$ is what is usually denoted as the spectrum of the observable f . More generally, however, an observable represents a mapping from a set of states of a system S to a set of attractor states of some other system with which S can interact.

Clearly, if our only access to the system S were through the single observable f , we could not distinguish two states s and s' for which $f(s) = f(s')$. Thus, we would in fact not be observing S itself, but rather a quotient set S/R_f , where R_f is the equivalence relation on S defined by writing $s R_f s'$ if and only if $f(s) = f(s')$. By definition, there is a 1–1 correspondence between S/R_f and the spectrum $f(S)$; in these circumstances, $f(S)$ would be for us “the state space” of the system S .

Now $f(S)$ is a set of real numbers, and hence comes equipped with a variety of natural structures. In particular, $f(S)$ is a metric space. We can employ such structures in $f(S)$ to *impute* corresponding structures to S/R_f , and thence to S itself. In particular, via the metric structure on $f(S)$, we can say that two states s, s' of S are “close” if the corresponding values $f(s), f(s')$ are close in $f(S)$. It cannot be too strongly emphasized, however, that such a topological structure is not intrinsic to S , but is imputed to S through a process of system description derived ultimately from observation in the fashion we have described.

Suppose now that we are given another observable g . We can repeat the above argument; g can be regarded as a mapping $g : S \rightarrow \mathbb{R}$ with spectrum $g(S)$; this spectrum is in 1–1 correspondence with the quotient set S/R_g , and we can impute another topology to S/R_g , and thence to S , through the metric properties of $g(S)$. Using the observable g alone then, we have another “state space” representation of S .

We can now ask: how does the description of S obtained from the observable f compare with the corresponding description obtained with the observable g ? We shall consider here primarily the metric properties, in the following form: if $f(s')$ is close to $f(s)$, under what circumstances will it be true that $g(s')$ is also close to $g(s)$? Stated another way: if s' “approximates” to s under f , when will it also “approximate” to s under g ?

This kind of question is closely related to the compatibility of the mapping g with the equivalence relation R_f ; i.e. the capability of g to distinguish states indistinguishable (or approximately so) under f . Basically, we proceed as follows. Given a state s in S , consider the set of all states s' for which $|f(s) - f(s')|$ is small.

Look at the image under g of this set of states. If this image lies in a sufficiently small neighborhood of $g(s)$, we shall say that s (or more accurately, its equivalence class under f) is a *stable point* of g with respect to f . It is clear that the set of all stable points of g with respect to f comprise an open set in S/R_f , under the topology coming from $f(S)$. The complement of the set of stable points will be called the *bifurcation set* of g with respect to f . Obviously, near a bifurcation point, the proximity of two states s, s' of S as viewed by the observable f does not imply their proximity as viewed by g ; at a stable point this implication does obtain. Thus, on the stable points the f -description may be replaced by the g -description; on the bifurcation points it may not be. Stated another way: on the stable points, the g -description conveys essentially the same “information” as does the f -description, and is hence redundant to it; on the bifurcation points, the g -description conveys “new information”, distinct from that conveyed by the f -description.

In the discussion of the previous paragraph, we can interchange the roles of f and g , and obtain the dual concept of the stable points and bifurcation points of f with respect to g . These represent complementary subsets of S/R_g (or $g(S)$), and are thus generally quite different from the corresponding subsets of S/R_f considered in the preceding paragraph. Thus, given a pair of descriptions, we obtain two distinct notions of stability and bifurcation, depending on which of the descriptions is chosen as the reference.

To illustrate these concepts, let us look at a well-known mathematical example. We may describe a dynamical system in two distinct ways: (a) in terms of a vector field on a manifold, or (b) in terms of the attractors of the system. Invariably the vector field description is taken as the reference; thus we say that two dynamical systems are close if their vector fields are close in some appropriate norm. The problem of structural stability revolves around determining when it is the case that two dynamical systems whose vector fields are close are also close in terms of their attractors. The implications of structural stability (e.g. in terms of the “robustness” of dynamical descriptions of real systems) are well known.

On the other hand, we may interchange the roles of the two descriptions, and refer the vector-field description to that involving attractors. Intuitively, we would then ask: under what circumstances is it true that closeness in terms of attractors implies closeness of the corresponding vector fields in some norm? Such a question has profound implications, e.g. for modelling and simulation; it arises naturally out of the preceding considerations, but as far as we know it does not appear to have received any systematic study.

Before proceeding to some simple applications of these ideas, let us draw one elementary consequence from them. Suppose that f and g are two observables such that the bifurcation sets of f with respect to g , and of g with respect to f , are empty. Under these circumstances, it is appropriate to say that the two observables are *equivalent*; with respect to metric properties the two observables are everywhere

interchangeable. Moreover, in these circumstances, the relation between f and g is one of *conjugacy*; i.e. we can establish a commutative diagram of the form

$$(1) \quad \begin{array}{ccc} S & \xrightarrow{f} & S/R_f \\ \phi \downarrow & & \downarrow \psi \\ S & \xrightarrow{g} & S/R_g \end{array}$$

which allows us to “translate” the f -description into the g -description. This is again what we would expect from a study of purely mathematical examples of the concepts of stability and bifurcation. This equivalence (between *observables* rather than between states) will become important to us subsequently.

To conclude this section, we may note that the results we have obtained for descriptions arising from single observables may be generalized to descriptions involving any number of observables. To illustrate this, let us indicate how we may construct a more comprehensive description from a pair of observables f, g than that arising from either observable alone.

The utilization of a pair of observables essentially allows us to define a new equivalence relation R_{fg} on S , where we define $R_{fg} = R_f \cap R_g$. We now observe that we can always define a mapping

$$\theta : S/R_{fg} \rightarrow f(S) \times g(S)$$

which is in general 1–1 and *into*. This map arises from the fact that every equivalence class in S/R_{fg} is the intersection of a unique class in S/R_f and a unique class in S/R_g ; we associate each of these classes with the corresponding elements in $f(S)$ and $g(S)$ respectively. The image of this map corresponds to a “two-dimensional state space”, in which the observables f and g play the role of “state variables”. It may be noted that the map θ is onto if and only if every R_f -class intersects every R_g -class and conversely; i.e. iff the respective bifurcation sets are maximal. If these bifurcation sets are both empty, then as we would expect, the image of θ collapses to a one-dimensional subset of $f(S) \times g(S)$. This kind of representation can be extended in the obvious way to any number of observables. In each case, we obtain a topological space, in which the arguments given above can be repeated word for word.

Fuller details may be found in a forthcoming monograph [1].

APPLICATION: ARE BIOLOGICAL DESCRIPTIONS
REDUCIBLE TO PHYSICAL ONES?

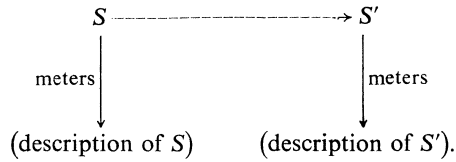
The prevailing idea among many biologists is that all biological descriptions are ultimately effectively reducible to physical ones; or even more strongly, that all biological descriptions are effectively derivable from physical ones. In the present section, we wish to explore how this idea can be tested, in the context of the discussion presented above.

To begin, let us cast the reductionistic hypothesis in terms of observables. A biological system, such as an organism, is surely also a physical system, and hence may be described in terms of the traditional observables with which physics is concerned. A dominant role here is played by the energy (Hamiltonian) of the system. On the other hand, the biological behaviors of the organism can be described phenomenologically; the ingredients for such descriptions are new observables of a fundamentally biological character. The reductionistic assertion is that each phenomenological observable arising in a biological description can be expressed in terms of the underlying physical observables. From this we can conclude that *such biological observables cannot bifurcate with respect to the underlying physical ones*. If such a bifurcation can be demonstrated, we could conclude that the corresponding biological observables could not be expressed as functions of the underlying physical ones, but rather comprise a logically independent mode of description of our system near the bifurcation points.

As we have defined it, observables are simply quantities which are capable of inducing dynamics on other systems, such as meters. If we are given a system S , then the characterization of S as a physical system is obtained by causing the states of S to interact with appropriate meters, which in effect evaluate physical observables on these states. In this way, as indicated above, we obtain a description of S as a physical system.

Now let us suppose that we use the states of S to induce dynamics on some other system S' . By definition, this dynamics must be expressible in terms of one or more observables of S . The question is whether the observables of S responsible for inducing the dynamics on S' are the same ones as we measure when we characterize the states of S with our meters (or more generally, are definite functions of these observables).

To answer this kind of question, we must generate two descriptions of S , which are to be compared. One description of S is already given; it arises from the set of meters through which we physically characterize the states of S . Further, we can obtain a second description of S , through the fact that its states induce dynamics in S' . For we can also characterize the states of S' through the employment of the same meters which characterize the states of S . Schematically, we have a diagram of the following form:



Here the dotted arrow represents the association of a state of S with an asymptotic state (attractor) of S' generated by the induced dynamics. If we interpret the description of these asymptotic states of S' as also being descriptions of the states of S which generate them, we have the two descriptions of S which we require. One of these descriptions is obtained directly from our meters; the other involves the dynamics induced by S in S' , and hence essentially involves those observables of S which generate this dynamics.

Clearly, if the second description bifurcates with respect to the first, it follows that the dynamics induced by S on S' involves observables distinct from those measured by our meters. Furthermore, these new observables are not reducible to those we measure directly, at least on the bifurcation points. These “new” observables must then enter as independent elements of system description, on exactly the same footing as those defined by our meters. Indeed, we may use the dynamics induced by S on S' to construct a *new meter*, in terms of which the observables of S which generate the dynamics may be defined. Such techniques of “bio-assay” are in fact widely used to measure the activities of organic substances, such as hormones.

It then becomes an empirical question to determine whether the observables manifested in biological interactions are distinct from those appearing in our physical descriptions of the system. A good place to look for such new “biological” observables is in situations involving specificity or discrimination mechanisms. We suggested long ago [2] that primary genetic processes would provide good candidates for the isolation of such observables (although the character of the argument given therein was quite different). More recently, Comorosan has applied the same circle of ideas to an empirical study of the observables involved in enzyme-substrate interactions [3]. From his work, he concludes that simple substrates for enzymes may exist in classes of states which appear indistinguishable to our physical meters, but which may be split (discriminated) by enzymes; the enzymic discrimination appears as a small but significant modification of reaction rate. Independent experimental confirmation of this work has been reported [4], and further study would be desirable.

The implications of such considerations for reductionism in biology are obvious. It should be stressed, however, that there is nothing “unphysical” about such new biological observables, just as there was nothing “unphysical” about, e.g., spin. It is perhaps not surprising to find that interactions between complex systems reveal capabilities not manifested on interaction with simple systems; the concept of bifurcation of descriptions provides an explicit probe of these capabilities, and of how they are logically inter-related.

ABSENCE OF BIFURCATION: MODELLING AND SIMILARITY

In the present section, we wish to consider some of the ramifications of diagrams like (1), which represent the context for the development of concepts of similarity between systems.

In general, suppose that $f, g : A \rightarrow B$ are conjugate maps, related by a commutative diagram of the form

$$(2) \quad \begin{array}{ccc} A & \xrightarrow{f} & B \\ \phi \downarrow & & \downarrow \psi \\ A & \xrightarrow{g} & B \end{array}$$

We shall interpret such a diagram as follows: the expression $b = f(a)$ is *invariant* to

- (i) the replacement of a by $\phi(a)$;
- (ii) the replacement of f by g ;
- (iii) the replacement of b by $\psi(b)$.

We shall introduce the following terminology: for a in A , the element $\phi(a)$ will be called its *corresponding element*; likewise for b in B , $\psi(b)$ will be its corresponding element. Then the assertion of conjugacy between f and g means precisely that corresponding elements are mapped by g onto corresponding elements. The invariance of the relation $b = f(a)$ to these replacements is the abstract analog to the *Law of Corresponding States* in thermodynamics.

Now let us suppose that S is a system, and that we are given two descriptions $F = (f_1, \dots, f_m)$, $G = (g_1, \dots, g_n)$ of S , where the f_i and g_j are observables. Suppose further that the set of bifurcation points of the G -description with respect to the F -description is empty. Then as we have seen, there is a sense in which the F -description implies the G -description on every state of S . We saw also that (under mild assumptions) each such description can be regarded as giving rise to a manifold, in which the f_i and g_j respectively can be regarded as local coordinates. Under these circumstances, we can write a functional relation of the form

$$(3) \quad (g_1, \dots, g_n) = \Phi(f_1, \dots, f_m)$$

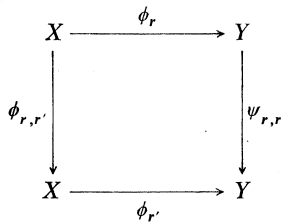
valid for every state s in S . Such a relation can be regarded as an *equation of state* for S . It should be noted that the mapping Φ is not itself a system observable, but rather expresses a relation between observables (i.e. between descriptions of S).

In general, a single function of m variables can be regarded as a 1-parameter family of functions of $m - 1$ variables, indexed by the range of one of the arguments.

Thus in particular, $\Phi(f_1, \dots, f_m)$ can be regarded as a 1-parameter family of functions

$$\Phi_r(f_2, \dots, f_m)$$

where the index r runs through the spectrum $f_1(S)$ of f_1 . Suppose it is the case that all the functions in this 1-parameter family are conjugate (the condition under which this is true can be expressed in terms of the bifurcation set of f_1 with respect to each of the other f_i); then given any two elements r, r' in the spectrum of f_1 , there is a diagram of the form



with the properties we have noted above (here X is the manifold determined by the observables f_2, \dots, f_m , Y is the manifold determined by the observables g_1, \dots, g_n).

In terms of the system S , this process amounts to regarding S as being composed of a 1-parameter family of (sub)systems S_r , each of which is described by the corresponding equation of state determined by Φ_r . The assertion that the Φ_r are all conjugate amounts intuitively to asserting that all the systems S_r are *similar*; this in turn means the following: the replacement of a given S_r by $S_{r'}$ can be “annihilated” by replacing corresponding elements by corresponding elements in the equation of state; i.e. by coordinate transformations in the domain and range of the Φ_r .

We can imagine this process continued, in such a way that the original function Φ can be expressed as a p -parameter family of conjugate functions of $m - p$ variables, of the form

$$\Phi_{r_1 \dots r_p}(f_{m-p+1}, \dots, f_m)$$

and that p is maximal for this property (i.e. any set of $p + 1$ of the observables f_i gives rise to non-conjugate functions). Then the system S has accordingly been decomposed into a p -parameter family of systems $S_{r_1 \dots r_p}$, and all of these systems are similar. Once again, this means that an arbitrary transition $(r_1, \dots, r_p) \rightarrow (r'_1, \dots, r'_p)$ can be annihilated by replacing corresponding elements by corresponding elements.

It may be noted that the above considerations can be regarded as an abstract form of the “Buckingham Π -Theorem” [5] which was originally obtained through very special dimensional arguments.

Another way to express the above construction is the following: the bifurcation set of the description of S obtained from the observables (f_{m-p+1}, \dots, f_m) with

respect to the description obtained from the observables (f_1, \dots, f_p) is empty, and the value p is maximal for this property.

Now let us introduce some picturesque but not entirely unjustified terminology. We shall call the set of parameter values r_1, \dots, r_p the *genome* of the corresponding subsystem $S_{r_1 \dots r_p}$; the domain of the map $\Phi_{r_1 \dots r_p}$ will be called the *set of environments* of the system, and the range of this map will be called *the set of phenotypes*. Then the equation of state asserts simply that a specification of a particular genome in a particular environment uniquely determines the corresponding phenotype.

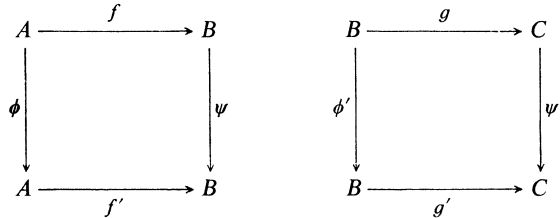
The D'Arcy Thompson "Theory of transformations" [6] asserts essentially that closely related species are similar. In our terminology, this translates into the assertion that if the genomes of two systems are close in some appropriate norm, then the phenotypes are corresponding. This formulation permits a number of interesting and potentially testable conclusions to be drawn; space precludes us from entering upon a fuller discussion here, but details may be found elsewhere [7]. Moreover, the above discussion allows us to meaningfully extend the functional concepts of genome and phenotype to non-biological systems; this permits, for example, a better understanding of the significance of non-biological morphogenetic metaphors, such as critical phenomena and diffusion-reaction mechanisms, which seem at first sight to be devoid of any plausible genetic component.

Another facet of the above formulation which may be mentioned is the following: if we keep the genome fixed and modify the environment, we obtain a corresponding change in phenotype governed by the equation of state. Likewise, if we keep the environment fixed and modify the genome, we again obtain a change in phenotype. Such phenotypic changes can be regarded as *adaptations* of the phenotype to the imposed modifications. They are imposed by the requirements of invariance of the equations of state. In general, if we study what varies when a perturbation is imposed on a biological system, we obtain a theory of adaptation; if we study what remains invariant under such a perturbation, we obtain a theory of homeostasis. What we wish to stress is that adaptation and homeostasis represent different aspects (descriptions) of the same basic phenomena.

Let us now turn briefly to the concept of modelling and model systems. Intuitively, we may say that some structure S' is a model for another structure S if, in a given set of circumstances, S' may be substituted for S with no observable change; i.e. if this substitution is *invisible* under the given circumstances. Thus, given an observable $f : S \rightarrow \mathbb{R}$, we may replace a state s by any state s' for which $f(s) = f(s')$; under these circumstances we may say that s' models s . Likewise, we may replace an observable by a conjugate observable, if we simultaneously replace each element of the domain and range by the corresponding elements. We may likewise replace a system by a *similar* system. It is clear that the formalism we have developed above, based on the comparison of system descriptions, is likewise a general theory of modelling. As noted above, the appearance of bifurcations indicates where a modelling relation

breaks down. However, it is equally significant to note where such a relation is maintained; this is the province of the concept of similarity.

Let us conclude with one final variation of the diagram (2). Let us suppose that we have a pair of conjugacy relations, of the form



so that we may say that f, f' are similar, g, g' are similar. As noted above, this means that we can replace f by f' , and g by g' , as long as we also replace corresponding elements by corresponding elements, and observe no change. Now, however, let us compose the maps f and g , and let us ask whether the composite gf is conjugate to the composite $g'f'$. It is evident that the conjugacy of the composites does not follow in general from the conjugacy of the factors. Moreover, even if the composites are conjugate, the elements of A and C which were corresponding in the diagrams considered separately will no longer in general be corresponding when the maps are composed. This simple observation throws another kind of light on the problem of reductionism: in general, the availability of models (descriptions) of the components of a composite system does not allow us to construct a model for the composite system itself. Conversely, a model for a composite system does not allow us to construct models for the components. Hence we see in a particularly stark way the difficulties faced in the analysis and the synthesis (design) of complex systems. Furthermore, the failure of conjugacy to be preserved under composition of mappings raises some deep questions of a category-theoretic nature. In category theory, composition of mappings is the basic operation, which is preserved by functors. Since conjugacy is not preserved under composition, it cannot be a functorial relation, and hence is not “natural” in the category-theoretic sense. Therefore it appears that category theory cannot by itself provide us with an appropriate tool for the analysis and synthesis of complex systems.

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