

SUPERVENIENCE AND REDUCTION IN BIOLOGICAL HIERARCHIES

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1. Introduction

Supervenience is a relationship which has been used recently to explain the physical determination of biological phenomena despite resistance to reduction (Rosenberg, 1978, 1985; Sober, 1984a). Supervenience, however, is plagued by ambiguities which weaken its explanatory value and obscure some interesting aspects of reduction in biology. Although I suspect that similar considerations affect the use of supervenience in ethics and the philosophy of mind, I don't intend anything I have to say here to apply outside of the physical and biological cases I consider.

The main point of this paper is that there is a property of biological systems which makes it both misleading and inappropriate to reduce central biological phenomena to the properties of underlying components. Despite this, reductive explanation has been a major source of innovation in biological theory. The apparent tension can be resolved if underlying properties are explanatorily relevant to the higher level phenomena even though the latter are not strictly reducible to the former. Supervenience, I will argue, is not robust enough to deny reduction while supporting explanatory relevance. The required property entails supervenience, but

is not entailed by it. I call this property *cohesion*. Roughly, a system is cohesive if there are causal interactions among its parts which make it insensitive to fluctuations in the properties of its lower level components. When a system is cohesive, these fluctuations are irrelevant to its state description, and it is both pointless and misleading to describe the system in terms of the properties of its lower level components.¹

I will first discuss the nature of biological hierarchies, and will then distinguish the ontological from the epistemological and pragmatic aspects of reduction. My concern will be limited to the ontological aspects. I will not be concerned here with theoretical reduction. It is a reduction relation between theories, which are conceptual entities. Examples of theories in biology are Mendelian genetics, molecular genetics and population biology. Ontological reduction has traditionally been a necessary condition for theoretical reduction in

¹ This principle is central to the entropic theory of evolution proposed by D.R. Brooks and E.O. Wiley (Brooks and Wiley, 1986), and to the thermodynamic approach to ecology developed by R.E. Ulanowicz (1986).

empiricist philosophy of science² This stems from a formalistic view of reduction and meaning, and the correspondence presumed between theories and the world. Although there is an intuitive reductive relationship between molecular and Mendelian genetics, it is not the strict reduction of the empiricists (Hull, 1979). Minimally, molecular genetics can help to explain certain aspects of Mendelian genetics. I call such explanations *reductive explanations*. Reductive explanation is possible without strict ontological reduction. In the remainder of this paper "reduction" will refer to strict reduction.

Next, I will distinguish two types of reduction: *microreduction*, which is an identification of higher level phenomena with some composition of properties of entities lower in a hierarchy, and *macroreduction*, which is an identification of properties at the same level in a hierarchy, where the properties differ only in their description. I will then recount the origins of the concept of supervenience, and how it has been applied in biology. Next, I will discuss the case of the explanation of thermodynamics in terms of statistical mechanics, and derive some lessons for biology. Finally, I will show why cohesion blocks reduction but allows the explanatory relevance of lower levels, and will end with some examples.

2. Biological Hierarchies

It is fairly evident that biological systems are hierarchically organized, though the exact nature, and even the number of

² Ontological reduction is not sufficient for theory reduction, since two theories may not say the same things about the same entities. Also, the constraints on reduction of concepts are generally stricter than for reduction of their extensions, since the role a concept plays in particular theories must also be reduced.

independent hierarchies might be in doubt. As a first approximation, we might pick out the levels in Figure 1. No doubt I have left

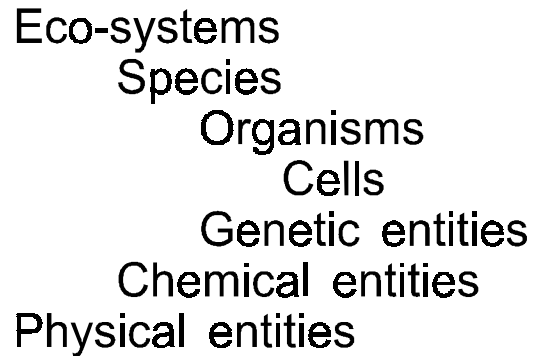


Figure 1

out some levels in this simplified scheme. Even so, it should be apparent that it is natural to describe each level as being composed of components from lower levels, and that there is a tendency to conceive each level as being "nothing but" a manifestation of the next lower level (with possible independent contributions from still lower levels).

Some terminology will be helpful here: If something belongs to a relatively higher level it will be termed *macro*, while if it belongs to a relatively lower level it will be termed *micro*. The relation between macro and micro levels can be characterized in terms of spatial and temporal containment (Salthe, 1985). Elements of the lower levels are smaller than the elements of the higher levels that contain them, and generally they have a briefer existence. There are exceptions to the temporal part of this rule; for example, atoms last longer than organisms, and genetic information can last longer even than species. I know of no exceptions to the spatial part of the rule.

There appear to be at least two separate biological hierarchies (Salthe, 1985; Eldridge and Salthe, 1984; Eldridge, 1985): (1) the *genealogical hierarchy*, which is a

hierarchy based on genealogical processes such as reproduction, epigenesis and speciation, involving DNA, genes, cells, organisms and species, and (2) the *ecological hierarchy*, which is based on ecological processes such as competition, selection and adaptation, but also includes processes inside the organism and even the cell. The two hierarchies can interact in complex ways.

The level that a property belongs to is determined by the level at which the relevant interactions occur. For example, it is often thought that fitness is a property of organisms, but since fitness is a relation between an organism and an environment (Brandon, 1978; Mills and Beatty, 1979), it is really a property internal to ecosystems. There is a property of each organism which explains its fitness in a given environment, but this property, whatever it is, is not itself the organism's fitness. Another example is the determination of characters. This is often represented as being a property of DNA alone, but it does not require careful consideration to recognize that developmental conditions, both internal and environmental, are also important.

Though both hierarchies can be conceived of as composed of individuals, the genealogical hierarchy is most naturally conceived of as a hierarchy of individuals, whereas the ecological hierarchy is most naturally conceived of as a hierarchy of processes acting on the individuals of the genealogical hierarchy (Eldridge, 1985). Connections both between members of a level of the genealogical hierarchy and between levels are ecological processes (which, of course, depend on the properties of the members of the genealogical hierarchy). The hierarchy I listed above is a hierarchy of individuals.

Reductionism in its usual guise holds that macro entities are "nothing but" micro entities or combinations of micro entities, and that macro properties are nomologically coextensive with micro properties or

combinations of micro properties³. Reduction, then, requires that micro phenomena determine the corresponding macro phenomena. Proponents of supervenience accept this requirement, but deny the cogency of the identifications reduction requires. The issue of reduction has been discussed primarily with respect to the relation between fitness and underlying physical or organismic properties (Brandon, 1978; Rosenberg, 1978, 1985; Sober, 1984a), and the relation between Mendelian genetics and molecular biology (Hull, 1974, 1976a, 1979; Kimbrough, 1979; Kitcher, 1982; Rosenberg, 1985). In the latter case, the ontological reduction required is between Mendelian genes and segments of DNA. We could also ask whether eco-systems are just collections of populations, whether species are really just collections of organisms, and whether organisms are really just collections of cells.

The reductionist position has been taken on each of these questions. In each case it holds that the appearance of independent levels is an illusion resulting from our inability to discover and analyze the true causal processes at the micro level. On this view, the macro phenomena are at best epiphenomena of the micro level. Biologists have generally resisted reductionism. If this is not merely a prejudice, there must be some property of the systems found in biological hierarchies which blocks reduction.

³ It was once common in the literature to distinguish between entity reduction and property reduction. This is a red herring. The identity of neither properties nor individuals can be decided conclusively on the basis of our conceptions of them, but only on the basis of empirically established laws. I will have more to say about this below.

3. Importance of the Ontological Problem

The reduction issue might seem academic in biology, since we do not presently know the details of how the different levels are related, nor are we likely to in the foreseeable future. It might seem to be a moot point whether reduction is ruled out (where it is ruled out) because of the limitations of our current theories and knowledge, or whether there are fundamental properties of biological systems which make reduction impossible or inappropriate. I think that the second possibility is interesting in itself, and should be addressed directly.

There are cases from theoretical biology which illustrate the importance of both reductionist and anti-reductionist positions. The ontological status of species has consequences for both systematics and evolutionary theory. The conception of species as individuals (Ghiselin, 1966, 1974, 1987; Hull, 1976b, 1978, 1987), which is anti-reductionist in spirit, strongly supports phylogenetic systematics against pheneticism or reformed cladism (Ridley, 1986). The entropic theory of evolution (Brooks and Wiley, 1986; Collier, 1986), which equates evolution with a non-equilibrium increase in certain informational measures of historical individuals, unlike the selectionist view of evolution as an approach to genetic equilibrium after either environmental or genetic change in a population (Ginzburg, 1983), requires that species are individuals with their own peculiar causal properties and internal organization.

There are many examples on the reductionist side. An understanding of micro processes can lead to restrictions on possible macro processes which would be difficult to prove just by examining macro phenomena. One important example is the influence of studies of the reproductive physiology of the cell on what we now call transmission genetics. Lamarckian mechanisms of evolution were finally rejected at the turn of

the century only after studies in cell physiology and differentiation in the early development of the organism led Weissmann and de Vries to recognize that Lamarckian genetics was incompatible with the underlying physiology (Churchill, 1970; Mayr, 1982: 693-726). This work led to the revival of Mendelian genetics, which seems to have been incapable of surviving merely on its own merits. Other examples of successes resulting from reductionist tendencies are the recognition of the cell as the fundamental physiological unit (now incorporated into virtually every contemporary introductory biology text), which is at odds with the conceptions of the mid-eighteenth century (Churchill, 1987), and reductive explanations stemming from the recognition that traits are molecularly determined and from the breaking of the genetic code.

Although reductionist moves have led to changes in our understanding of genetics, physiology and evolutionary theory, genes have not been reduced to the entities of either cell physiology or molecular biology (Hull, 1976a, 1979; Kimbrough, 1979; Rosenberg, 1985). An understanding of micro processes can lead to reductive explanations even without strict reduction. Furthermore, the anti-reductionist example of the status of species as individuals shows that insight can be gained by resisting reduction. Similarly, the reduction of natural selection to processes at the molecular level would tend to obscure the important role that Mendelian genes and phenotypic traits play in adaptation. The details of the molecular processes involved in adaptation are not really relevant to understanding the process of adaptation, though certain general facts about DNA, such as the insensitivity of its information to direct physiological and environmental influences, are very relevant. The gross facts of the nature and function of DNA explain why Lamarckian adaptation seldom, if ever, occurs.

On the Hempelian covering law model of explanation (Hempel, 1965), laws can be used to explain other laws if and only if the laws to be explained can be derived from the explaining laws together with suitable auxiliary assumptions. This is really no different from reducing the laws to be explained to the explaining laws via empirically established bridge principles. Thus, the Hempelian model of explanation does not allow us to resolve the tension pointed to in the last few paragraphs. This leaves us with a puzzle: How can the Hempelian model of explanation be weakened to allow a suitable account of explanation without reduction? Unfortunately, I will not be able to answer this question here. I will address a subsidiary question: What is it about biological systems which prevents reduction but allows reductive explanation? The answer, I will argue, is to be found in the nature of cohesion.

4. Inter-level vs. Intra-level Reduction

Reduction has an undoubted virtue in explanation. If some phenomenon is to be explained in terms of something else, the two must be commensurate. Otherwise there will always be some element of mystery in the explanation. Reduction guarantees that both the phenomenon to be explained and the explanation can be understood in the same terms. The discussion of reduction in the previous sections has been restricted to microreduction. It is not the only form of reduction, however. Hooker (1981) has suggested that properties can be reduced at the same level, what I have called "macroreduction". Reduction within levels has the same advantage as reduction between levels of guaranteeing commensurability.

Hooker notes that some properties are more determinate, while others are more determinable. For example, being red is more determinate than being coloured, but is more determinable than being one of the

innumerable shades of red. If something is a certain shade of red, it follows that it is red, and also that it is coloured. Many physical properties, Hooker believes, come in various degrees of determinateness. To reduce a mental property to physical properties, we must choose physical properties which have a determinateness commensurate with the properties to be reduced. Macroreduction is not a reduction to components, but a reduction in general types of things. With microreduction we eliminate some particular things from our ontology by showing that they are just combinations of things that we are already committed to. Macroreduction doesn't reduce the number of particular things; it reduces the number of types of things. A successful macroreduction shows that two types of things which we took to be different types of things are really the same type of thing. (Microreduction has this reduction of types as a side effect.)

For example, suppose a device R is "on" if and only if at least one shade of red is present. R is a redness detector. Assume that shades of red are different if and only if they are distinguishable, i.e., there is some device S that can distinguish them. Microreduction of redness to its shades is then impossible, since individuation of shades of red cannot generally be done: It is possible that shades A and B, A and C, B and C, B and D, and C and D are each pairwise indistinguishable, yet shade A can be distinguished from shade D. It is undetermined whether B or C are identical with A, or with each other, though not both are identical with A. There might be some E, distinguishable from B but not from C which allows B and C to be distinguished. This method can break down eventually, however, since only a finite number of distinguishable shades exist, and eventually there will be no new shades to allow further individuation. It would be absurd, however, to say that shades of red are incommensurate with redness. The solution is to identify redness with a range of shades. R is sensitive to a range of shades of

red, i.e., to red. Instead of reducing red to a construct of shades of red (microreduction), it is reduced to a macro property of its shades, i.e., a range. We don't need redness in addition to its shades and their properties, so we can reduce the number of types of things. This example is somewhat artificial, but I think it illustrates the nature of macroreduction.

Since explanation requires commensurability, which in turn requires some sort of reduction, and microreduction seems to be unsupportable in at least some interesting cases in biology, the need to legitimize successful reductive explanations suggests that we should look for macroreductions. We need, then, to characterize cases in which 1) microreduction is impossible or at least unhelpful, 2) micro processes are explanatorily relevant, and 3) macro reduction is possible. Part of the problem is knowing where to look to satisfy these desiderata.

If reducibility is a property of our representations of systems, then the proper place to look for the reasons for reducibility is in our representations and their relations to each other. Typically, discussions of supervenience and reduction have concerned themselves with the existence or non-existence of bridge laws correlating biological with micro properties as they are represented in our current theories. The strongest form of correlation is conceptual, based on meaning postulates. The absence of conceptual relations between macro and micro properties doesn't say much about the world unless we assume that our conceptions accurately portray the world. This assumption, however, needs justification. There is no particular reason to believe that the limits of our current understanding of biological and physical properties reflect the limits of possible relations between these properties.

Likewise, the absence of nomological relations between macro and micro properties within our current biological theories doesn't

show that there are no such relations. It merely reflects the current state of our knowledge. Nonetheless, if we have looked for nomological relations and have not found them, we do have some *prima facie* evidence that the relations do not exist. Scientific arguments for the non-existence of something are inherently risky, though, since they may reflect our lack of skill or experience rather than genuine characteristics of the world. It would be better to base arguments for non-reducibility on a positive argument that biological properties have characteristics which prevent their reduction. I will show that cohesion undermines inter-level reducibility while still permitting macroreduction.

Supervenience, on the other hand, is too blunt an instrument on which to base the relationship between macro and micro properties. It might be that the supervenience of biological properties follows logically from our conception of biological and physical properties. If so, supervenience either holds trivially, and tells us little about micro reducibility, or else asserting that it holds begs the question of reducibility. Alternatively, supervenience might entail the impossibility of reductive explanations. I have argued that reductive explanations do not entail reducibility, and that we want to allow them in order to account for some important episodes in the history of biology. This latter account of supervenience, then, will not help us understand biology. The last possibility is to try to identify supervenience empirically. Rejection of this possibility will require a closer examination of what supervenience involves.

5. Supervenience

The concept of supervenience was designed to resolve a problem in a certain approach to value theory. Moore argued that although values are non-natural properties, the same natural circumstances determine

the same ethical properties. There can't be two possible worlds which are the same in all factual respects, but differ in ethical properties. For example, there could not be a world in which Francis of Assisi has all of the factual properties that he has in this world, but in which he is a bad person. Ethical properties are determined by natural properties, but cannot be derived from them. Similar arguments have been made for aesthetic values. The reasoning behind this distinction between the determination of values by natural properties and the derivability of values from natural properties is based on the conviction that one cannot derive values from facts, together with the metaphysical principle that the facts about the world determine everything about the world. The determination of values by facts, together with their non-derivability from facts is called the supervenience of values on facts.

How something could be determined by but not derivable from is unclear. Giving the relation the name of supervenience does not really help with this mystery. Ruse (1986, this volume) agrees with the non-derivability of values from facts, but maintains that facts are nonetheless relevant to the explanation of values. I won't pursue the relation of facts and values further here, since it would take me too far afield, but will merely note that Ruse has called into question the necessity of derivability for explanation.

The next application of supervenience was to mental properties (Kim, 1978). The basic idea is that although each instance of a mental property is coextensive with some physical property, there is no physical property which is nomologically coextensive with any mental property. Although physical properties determine mental properties in each instance (as we can determine from the general metaphysical principle that the properties of the whole are determined by the

properties of its parts⁴), there is no way to determine solely from knowing which mental properties hold what the underlying physical properties are.

Fodor's distinction between token-token identity and type-type identity (Fodor, 1968; Block and Fodor, 1972) is useful for explaining the supposed situation. A token-token identity is an identity of instances, whereas type-type identities are identities of classes. It is possible for an instance of some type of thing to be the same instance of some other class of thing, although not all instances of the first class are instances of the second. To take a mundane example, a particular statue might be identical with a particular lump of clay (I assume their spatio-temporal boundaries are the same), but it is certainly not true that all statues are lumps of clay. Fodor holds that although every mental token is coextensive with some physical token, the physical tokens which can embody any mental type are limitless in their variety, thus there is no physical type which is nomologically coextensive with the mental type. This argument can be applied in the same form to the relation between biological and physical properties. I will argue below, however, that it is suspect for the case of microreduction. It does not apply to macroreduction.

Kim (1978) and Rosenberg (1978, 1985) use a semi-formal definition of supervenience which they use in psychology and biology respectively:

A family M of properties is
supervenient on a family N of
properties with respect to a

⁴ The characterization of the relationship as a whole-part relation might strike some as question-begging. The metaphysical principle can be replaced with an empirical generalization that macro properties are determined by micro properties (Kincaid, 1987)

domain D iff, necessarily, objects in D which share all properties in N', the Boolean closure of N, will also share all properties in M', the Boolean closure of M.]

This definition allows both reducibility and definability of the properties in M in terms of the properties in N'. In fact both reducibility and definability entail supervenience, because they require biconditional *bridge laws* between properties in M and N'. Note also that supervenience by this definition is reflexive, and may have symmetrical instances. This need cause no problems, but it would be neater if supervenience were antisymmetric. It is of course transitive.

If supervenience is to be non-trivial, the reducibility and definability of the properties of M in terms of N' must be ruled out somehow. Rosenberg (1985) proposes that reduction in biology is ruled out on practical grounds. Any reduction of Mendelian genes to molecules, or fitness to micro properties, would be so complex as to be unmanageable, and we don't need to carry out a reduction to develop the macro theory anyway. Rosenberg is certainly correct on both these points. Practical grounds, though, are not sufficient to rule out ontological reducibility. Rosenberg argues that ontological reduction is both a logical and physical possibility. It is a physical possibility because the size of the world is finite, and physical laws, insofar as they are biologically relevant, are deterministic, so there must be a finite number of physical instantiations of any of the macro properties (for the detailed argument, see Rosenberg, 1985: 62-64). Consequently, each macro property must be coextensive with some complex physical property. I find this argument unassailable without commitment to either indeterminism or the infinitude of the world. The major objection is that complex physical properties are not admissible if they involve long

disjunctions. I will give a counterexample to this complaint shortly.

I believe, however, that Rosenberg's implicit view that only the practical aspects of reduction are relevant to theory choice is wrong. As I argued above, questions of ontological reducibility can be relevant to the choice of biological theory. Furthermore, we should sometimes make the choice dictated by the anti-reductionist position. This choice can be justified on ontological grounds. Although I agree that microreduction is always an ontological possibility, for cohesive systems it requires specification of micro properties which are irrelevant to the specification of the state of the system.⁵

Sober (1984a: 48) uses a narrower definition of supervenience than Kim or Rosenberg:

A property supervenes on a set of physical properties iff:

- 1) The property is not itself physical, in the sense that different objects may share the property, but be physically different.
- 2) Two systems which are physically identical must both have or lack the property.

I presume that Sober means that a property is not physical if it is not type identical to a physical property⁶. This definition of supervenience rules out any sort of reduction,

⁵ Campbell (1974) suggested that inter-level reduction ignores two properties of biological hierarchies that he calls emergence and downward causation. My position is that it obscures the ontological basis of these properties.

⁶ Although Sober refers to Kim's paper, I doubt he has the same conception of supervenience in mind, since by Kim's definition supervenience is reflexive and allows reduction. For a physical property not to be physical would be absurd.

macro or micro. It is more restrictive than Kim's version, and correspondingly more difficult to establish.

Sober argues that fitness is supervenient because there are a wide variety of physical conditions underlying fitness. Unlike physical forces, which come in only four basic forms that are easy to determine, fitness is not so easily classified according to its physical source. If this is not merely a practical problem, the assumption of the physicality of each instance undermines Sober's position, since it guarantees, given the assumptions of finitude and determinism, that fitness in all its manifestations can be analyzed in terms of some complex property of the four forces. Many properties which are clearly physical, such as geological properties, are not at all easy to analyze in terms of the four basic forces. This is particularly true for geomorphological properties, whose explanation involves historical and statistical components.

Sober has replied to me in correspondence that he does not regard complex disjunctive properties as genuine properties. He wishes to use the Fodorian argument that a property (fitness in this case) which has a wide range of physical instantiations cannot be microreduced. I think he is wrong, as a simple counterexample will show. Take the property of being rugged, as mountains are rugged. There are an endless number of ways of being rugged, and no doubt there are myriads of rugged things in the universe. Furthermore, it is highly probable that no two of them are rugged in exactly the same way. Despite this, there is little doubt that ruggedness is a physical property, and that it is ontologically reducible to constituent physical properties which are not themselves ruggedness.⁷ It

⁷ This argument could be reproduced for the property of "having the energy E", or for a wide variety of other undoubtedly physical

might be objected that there is really no significant difference in the ways that different mountains are rugged. This is not likely to impress someone who has to negotiate a particular mountain on a regular basis, however. The ruggedness of each mountain is qualitatively different from every other, as a trip through any mountain range will quickly verify. In order to block this counterexample, Sober would have to show that fitness is not physical, but I don't see how this can be done without begging the question. Since each instance (token) of fitness is physical, there are good *prima facie* grounds for holding that the property itself is physical. It is difficult to imagine what sort of evidence could establish that fitness is not physical.

I do not deny that fitness has a characteristic that ruggedness lacks which makes reduction inappropriate, but that characteristic is not supervenience. Supervenience is simply not rich enough to do the job. Sober quotes Fisher (1930: 39): "Fitness, although measured by a uniform method, is qualitatively different for every different organism, whereas entropy, like temperature, is taken to have the same meaning for all physical systems." I find this quote ironic, since I believe that thermodynamic state variables are very similar to fitness with respect to ontological reducibility. I will turn to this in the next section.

7. Cohesion

Consider a thermodynamic system in a given state. According to statistical mechanics, the state of the system is determined by its microstate, but its state at a given time is compatible with a wide range of microstates. The state variables are

and reducible properties, but ruggedness is particularly evocative.

determined by statistical averages of the properties of the particles which comprise the microstate. The macrostate is supervenient (*sensu* Kim and Rosenberg) on the microstate. Typically, the microstate can fluctuate through a wide range while the thermodynamic state remains constant. It is in principle possible to determine the macrostate at a given time given the microstate, but not vice versa, since there is far more information in the microstate than in the macrostate. This extra information in the microstate is irrelevant to the macrostate, since it fluctuates uncontrollably (uncontrollable from the macrostate without modifying the macrostate, that is).

Prigogine (1962) has shown that it is possible to use purely mechanical arguments to show that only the statistical properties of the microstates of the system are relevant to the determination of the macrostate. In a wide variety of systems, interactions between the parts of the system allow it to satisfy the condition of dissipativity (Prigogine, 1962: 265-269). If this condition is satisfied, the system will evolve towards thermodynamic equilibrium, and the gross behaviour of the system is insensitive to the detailed motions of its parts. To reduce the macrostate to properties of the microstate, there is no need to reduce to the complete Hamiltonian of the microstate, but only to its statistical properties. The absolute properties of the microstate are irrelevant to the description of the macrostate. The appropriate reduction of the phenomenological state is not to the microstate, but an intra-level reduction to statistical properties of the microstate.

In thermodynamics, microreduction is inappropriate. We might ask why. The obvious answer lies in the legitimacy of taking the macrostate to be a real entity, with its properties being just the appropriate statistical properties of its microstates. What is the physical basis of this legitimacy? In the simplest case, a gas has a definite macrostate because it is contained in a relatively

impenetrable container. The causal interactions of the parts of the container allow it to act coherently to determine the macroscopic boundary of the contained gas. The capability of a system to interact with other macroscopic systems such that the statistical fluctuations of its microstate are irrelevant is the basis of the reality of its macrostates. The resulting stability can be due to either boundary or internal causes. These causes themselves can have a wide variety of physical bases. Whatever causes the stability of the macrostate in a given case, I call *cohesion*. If a system is cohesive, it is both pointless and misleading to microreduce it, although it may be useful and enlightening to macroreduce.

Consider a kite flying in the wind. The usual explanation for the kite's lift is that there is a pressure difference between its bottom and top sides. This pressure difference would have no effect, however, unless the kite held together as a cohesive entity. The kite acts as a macroscopic unit due to causal connections between its parts. Thus it is insensitive to microscopic fluctuations in the number of molecules hitting its two sides, and responds only to the average. It is also fairly insensitive to larger scale fluctuations in the wind which cause its parts to flap, and to the movement of its parts relative to each other, as long as these movements are not too large. The cohesion of the kite at the scale of the kite itself makes these smaller fluctuations irrelevant to the explanation of its gross behaviour. It might be possible to reduce the behaviour of the kite/air system to the micro level, but this reduction would not add anything that is not determined by the statistical properties of the kite and the air. Macroreduction is all we need. Microreduction would only add irrelevancies.

Notice that cohesion is a causal property of the system itself, not merely a property of our description or conception of the system. Admittedly, cohesion is subject to degrees, depending on the strength of the

causal interactions responsible for it. Also, choosing too short or too long a time scale for observation may make stability difficult to detect. Neither of these considerations undermines the objectivity of cohesion. The inappropriateness of microreduction of a cohesive system, then, is ontologically grounded. Although I have not shown that cohesion is the only property that makes ontological reduction inappropriate, it is difficult to imagine any other that would do the same job. I postulate then that a system is not microreducible if and only if it is cohesive. I extend this claim (it is not a definition) to properties in the obvious way: if a property of a cohesive system is insensitive to microscopic fluctuations because of causal connections in the system's boundary or among its parts, then it is not microreducible.

Following the lead of Prigogine (1962), we can see how microreductive explanations are possible without microreducibility. The mechanical properties of systems satisfying the "condition of dissipativity", together with macroscopic cohesion, allow us to ignore the details of the microstate in favour of its statistical properties in analysis of the system's thermodynamic behaviour. The general properties at the mechanical level explain the macroreducibility of the thermodynamic state, and also why microreduction would be inappropriate. Furthermore, a general understanding of the microscopic processes can place limits on possible macroscopic processes, and can explain why some macroscopic state transitions are possible (such as those involved in the formation of dissipative structures), but not others. It can also help to explain apparent exceptions to the macroscopic rules, such as Brownian motion. In none of these explanations, however, is a complete reduction to the micro level necessary or desirable.

The possibility of macroreduction turns the tables on the anti-reductionist. Fisher, ironically, turns out to be insisting on

the priority of micro properties in his rejection of a general (macroscopic) treatment of fitness. Ulanowicz (1986) has proposed that fitness can be treated this way. He attributes biologists' reluctance to treat their subject matter macroscopically to accidents of scale:

By and large humans observe the "microscopic" events in ecology; that is, the interactions between individual organisms. The lesson of statistical mechanics is that by aggregating events on the observable level, one might eventually infer some macroscopic (whole system) principle that becomes a significant addition to the body of thermodynamic laws. (1986: 26)

Both Ulanowicz (1986) and Brooks and Wiley (1986) have suggested additions to the body of thermodynamic laws which incorporate properties of, respectively, the ecological and genealogical hierarchies. These additions are continuous with prior non-equilibrium thermodynamics; there is no clear place where the old principles are relinquished and the new ones take over; the additions are integrated into the statistical theory of thermodynamics.

There is another reason, though, for reluctance to treat biological properties macroreductively: the functionality of biological systems. The subject of biological explanations is often particular adaptations in particular organisms. Statistical treatment of ecological and genealogical processes seems to make explanations of particular adaptations impossible, since they are micro properties of the system at its appropriate level of description, i.e., the ecosystem. The laws governing genealogy and ecology can give only a general pattern to be expected under various conditions, but not detailed predictions or explanations of the particular forms which are observed. Even if we could

give an account of fitness as a macroscopic physical property, it would not explain the details of the fitness of a particular organism, as Fisher desires. Such considerations can lead to pessimism about finding general biological laws. The problem is that particular instances are not appropriate subjects for scientific laws. Ulanowicz (1986: 61), recognizing that fitness is a property not of individual organisms, but of ecosystems, avoids this problem by defining a property of ecosystems that he calls *ascendency* which explains fitness (albeit statistically). Having treated ecosystems in a general way, he can apply the theory to particular ecosystems, and explain particular adaptations. The problem with conventional approaches to adaptation is that they focus on an inappropriate level.

Functionality resists microreduction because it depends on stability at the level at which the functional interactions occur. There must be enough stability in the face of structural changes at micro levels to allow the same process to achieve the same end. In order to achieve this stability, the system in which the functional properties are embedded must be cohesive enough to be resistant to micro fluctuations. Thus, if we want to understand a functional property like fitness, we must understand the system which provides the prerequisite stability. This stability is achieved through causal feedback as found in some types of networks (see Levy, this volume; Ulanowicz, 1986). Fitness cannot be explained in isolation, but must be understood as a network property. Attempts to reduce fitness to micro properties of organisms are totally inappropriate, and doomed to failure. Macroreduction of functional properties requires careful consideration of the appropriate level for reduction.

Consider the difference between the thrust and lift functions in a bird and an airplane. If we structurally decompose an airplane, we find that there are certain

structural components responsible for lift, and other structural components which are responsible for thrust. The functional decomposition and structural decomposition of the airplane are directly commensurate with respect to thrust and lift, and it is appropriate to microreduce the flight function of the airplane at least to the level of gross structural components. This is not true of the bird, in which the lift and thrust functions are combined largely in one structural component, the wing. Microreduction is not possible for the flight function of the bird, since the various functions of flight are carried out by a structurally integrated system. We can identify different properties of this system as the properties responsible for thrust and lift, but these properties are properties of an integrated system.

When analyzing functional properties in physical terms, it is important to choose levels of function and structure which are commensurate. Most discussions of the reduction of fitness have failed to recognize that fitness is only a component of a larger functional system which must be reduced structurally at a higher level than attempts to reduce fitness alone would suggest. This error, together with (and enhanced by) the bias towards regarding characteristics which we can most readily observe as the most important, makes biologists blind to macroreductive possibilities commensurate with physical theory.

I will now quickly examine some standard problems of reduction in biology using these concepts.

8. Examination of some reduction problems

Species as individuals:

Species are cohesive. Cohesion in species is generated by reproductive closure, which is a physical process involving the physical transmission of genes in mating and the transmission of the information in genes

in ontogeny. Species cohesion has two components: vertical, which is by descent, and horizontal, which is mostly due to sexual reproduction (Wiley, 1988). For sexual species, conspecificity is the closure of the relationship of *mutual fecundity*:

For individuals A and B there are a number (perhaps 1 or 0) of minimal sets of characters which allow A and B to successfully interbreed. Call the union of these sets the fecundity characteristics of A and B. If this set is non-empty, we can say that A and B are *mutually fecund*.

A species is insensitive to variation in its members as long as its cohesion is maintained. If cohesion is lost, the species is split. Because of its cohesion, a species cannot appropriately be reduced to the combination of its members. Thus species are individuals, not collections, classes or sets.

Fitness:

The cohesion of fitness depends on the maintenance of:

- 1) a relevantly stable environment
- 2) the genetic basis of the organism
- 3) its ability to pass its genes on to its offspring or to enhance the reproduction of individuals bearing the same genetic information
- 4) the integrity of the ontogenetic program which produces phenotypic traits from a particular genotype.

Disruption of any one of these will disrupt adaptive cohesiveness to some degree. In particular, condition (4) can fail if the environment of the gene during development is radically altered. The success of the ontogenetic program depends on more than DNA encodings. On the other hand, adaptedness is insensitive to many changes of environment, genome, and quirks of

development. This very rough sketch is indicative of the causal factors involved in the stability of fitness. I suspect the standard operationalist definitions of fitness (see Brandon, 1978) cannot sustain an adequate account of the cohesion of fitness, and may represent epiphenomena.

The fitness of individual organisms is a property of a larger system involving interactions between environment, organisms, and the genetic information of organisms. The major consequence of the fitness of an organism is the relative number of copies of its genes produced due to its causal interactions with components of its ecosystem in subsequent generations of the population of which it is a member. This can serve as a measure of the organism's fitness, but does not define it, since fitness is a propensity to have a certain effect. The actual result may be due to chance fluctuations. The propensity is stable with respect to these fluctuations, but the actual result is not. Even defining fitness as a propensity (Mills and Beatty, 1979), while a step in the right direction, is not satisfactory (see Rosenberg, 1982). To define fitness as an increased propensity to transmit copies of genes is not much better than to define opium's tendency to induce sleep as its dormitive virtue.

Intuitively, fitness is information about regularities in the environment stored in the genome that enhances the reproduction of the organism's genetic information. This involves a coherence between the information stored in the genome and the information in the environment. In information theory, this coherence is called the average mutual information. It is symmetrical for the environment and organism, and thus depends on both. Macroreduction requires an account of the information flows involved in physicalistic terms. Collier (1986, 1988) describes a suitable physical information theory compatible with thermodynamic principles, and Ulanowicz (1986) applies the notion of mutual information to the analysis

of ecological networks. This work suggests that a physicalist macroreduction of fitness is possible, probably in thermodynamic terms.

Mendelian genes to DNA:

Hull (1974, 1976a, 1979) argues that the relation between Mendelian genes and DNA structures is many-many, and that, although there is a molecular structure underlying each instance of a Mendelian gene, any microreduction would be so complex as to be useless. This many-many relationship ensures that even macroreduction would have to be complex. Hull (1976a) also suggests that any reduction will not involve an identity of natural kinds. Assuming supervenience, the only two possibilities allowed are either that Mendelian genes are not cohesive, but are illusory epiphenomena, or that they are cohesive, and the complex property required by macroreduction is, contrary to our intuitions, a natural kind. The value of population genetics suggests opting for the latter, but is not conclusive.

The functionality of Mendelian genes mitigates against microreduction. There is a stability in the relation between genes and phenotypic traits which suggests that the cohesion of Mendelian genes lies in the causal processes involved in ontogeny. The interaction between phenotypic traits and selective forces provides further closure. Genes are selected as units which produce phenotypic traits on which environmental forces can work with some degree of autonomy. As in the case of fitness, the macroreduction of Mendelian genes requires a reduction of the whole network of which they are a functional part. This network includes not only ontogenetic processes, but also ecological ones. Due to the role of selective forces in the cohesion conditions for Mendelian genes, it would be surprising if Mendelian genes mapped directly onto the natural structural decomposition of DNA molecules. Any mapping is likely to be quite

complex, and explicable only by taking ontogenetic and ecological processes into consideration. Again, the appropriate language for description of these processes is physical information theory and thermodynamics.

Organisms:

Although we all know that organisms are cohesive, it is very difficult to say in what that cohesiveness consists. We do know, however, that organisms (except of course unicellular ones) can survive large changes in their constituent cells (including transplants). This is complicated by the fact that brain cells are not replaced. It does seem likely, though, that the body could survive transplants of nerve tissue, and can certainly survive the loss of a good deal of brain tissue. The body is therefore not appropriately reducible to its constituent cells. Another reason to resist reduction is that the body performs as a functional unit in its interaction with the external environment (for the most part). The functional properties of the body are not commensurate with its structural decomposition into organs or cells.

Ecosystems:

Ecosystems are more than merely collections of populations, if we follow Ulanowicz (1986), who defines several properties of communities which are important for explaining their growth and development, but are not commensurate with structural decomposition into populations. The closure conditions for communities involve the exchange of information, energy and matter. Ulanowicz uses the resources of information theory and non-equilibrium thermodynamics to define ascendancy, which he equates with growth and development in ecosystems.

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