

Part VII

BIOLOGY

Natural Selection, Hypercycles and the Origin of Life¹

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1. Introduction

Over the last eighteen years Manfred Eigen and his co-workers have postulated a new theory about the origin of life on earth that has presented a detailed account of how many of the features of extant living organisms (such as a universal genetic code and protein-nucleic acid interdependence) might have arisen from purely physical interactions.² This theory is critically based on the special dynamical properties of certain chemical cycles called "hypercycles" which cause some of them to exhibit hyperbolic growth over time while undergoing selection. The purpose of this paper is to separate two aspects of this theory and then to study the first one in greater detail. The first aspect consists of a physical account of evolution by natural selection at the molecular level that depends only on the kinetics of certain chemical systems and can be applied to a variety of such systems. The second consists of the special dynamical properties that are exhibited when this account is applied, specifically, to hypercycles.

There are at least four reasons for making this separation. *First*, the separation of the various components of any theory which clarifies the relations between them is often of scientific and always of philosophical interest. *Second*, it is the first aspect of this theory alone that shows that, at the molecular level, purely physical interactions can cause the evolution of systems by natural selection in the sense that they satisfy the three criteria for such evolution laid down by Lewontin (1970). *Third*, it is the second aspect alone that makes this theory a theory of the origin of life. *Fourth*, the first aspect of the theory might well survive even if the general Eigen picture of the origin of life turns out to be unsatisfactory, that is, the second aspect of the theory turns out to be false, as has often been suggested.³ Besides the fourth reason above, there are at least three other reasons for concentrating on the first aspect of the theory as is done here. *First*, and this is an extension of the second reason listed above, explaining the mechanisms by which natural selection can occur, at any level, is of biological interest. *Second*, a physical explanation of natural selection, once again at any level, contributes to the program of finding physical explanation of biological phenomena, that is, explanatory reductionism, and is, therefore, of added philosophical interest.⁴ *Third*, at the molecular level, the level of this discussion, physical explanation of natural selection provides a *physical* warrant for functional explanations in molecular biology thereby also advancing the program of explanatory reductionism.

The separation between the two aspects of the Eigen theory of the origin of life is achieved here by the exposition, first, of a dynamical theory of chemical systems and then showing how this theory is applied to hypercycles. This is done simply by writing down phenomenological kinetic equations that make no assumptions about the underlying processes of the system (Section 2). Assumptions about the kinetics of the system are then introduced that result in evolution by natural selection. This is first done for an autocatalytic system which is, in many ways, the simplest system that exhibits such behavior (Section 3). Next systems that are catalytically coupled by having complementary replication are introduced and it is shown that the equations describing the dynamical evolution of the second system are formally identical to those of the first (Section 4). Hypercycles are then briefly discussed to show where they fit in the scheme of things and why they are plausible candidates as systems by which life originated on earth (Section 5). After this brief digression into hypercycles, a characteristic example of a functional explanation in molecular biology is introduced and the conditions for its adequacy explicated (Section 6). The physical theory of evolution by natural selection for systems with complementary replication, developed in Section 4, is then used to provide a tentative physical warrant for this functional explanation (Section 7).

2. Phenomenological Equation and the Criteria for Evolution by Natural Selection

The following two general assumptions are being made for the chemical systems being considered here. First, it is assumed that the system consists of a population of n molecules, each of which is a polymer of length ν built from λ types of monomer and an environment with a large supply of energy-rich monomers from which such polymers can be synthesized. Thus $N = \lambda^\nu$ types of molecules are possible in the population.⁵ Second, it is assumed that the system is isolated in the following specific sense: (i) it is confined to a given volume V and (ii) no polymers can enter the population from outside V though polymers can leave V , and thus leave the system. Now, let x_i be the number of polymers of the i -th type in the population. It is assumed that the population is large enough for all x_i to be treated as continuous variables.⁶ Let R^B_i be the rate of increase of the i -th type of polymer due to formation, R^D_i its rate of decrease due to decomposition and R^E_i its decrease due to emigration from V . Then:

$$(dx_i(t)/dt) = R^B_i - R^D_i - R^E_i \quad (\text{Equation 1}).$$

This is the basic phenomenological equation. No assumptions have yet been introduced about the form of any of the three rates occurring in the right hand side. Specific forms for these rates determine the kinetics of the system as, for instance autocatalysis discussed in Section 3 and complementary replication discussed in Section 4.

For each of these specific kinetic models, the task then becomes to show that the dynamical development of the system, simply because of the physical properties incorporated in the kinetics, obeys Lewontin's three criteria of evolution by natural selection: (i) Phenotypic Variation: Different types of individuals, termed "phenotypes," in the population have different structure and behavior; (ii) Differential Fitness: Different phenotypes have different rates of survival and formation in the environment; and (iii) Heritability of Fitness: There is a correlation between the fitnesses of an individual and those individuals formed as a result of interactions between that individual and other parts of the system (Lewontin 1970).

3. Autocatalytic Replication with Natural Selection

An autocatalytic process is one in which a molecular type catalyzes its own formation. It is assumed here that this catalytic process admits occasional errors (due to quantum-mechanical uncertainties) which lead to production of molecules of other types. It will be

assumed that RB_i has the form $A_i Q_i x_i + \sum_{j \neq i} \phi_{ij} x_j$. The first term represents correct autocatalysis. The nature of autocatalytic process requires that this term be a monotonically increasing function of x_i . It is being assumed to be linear here as a first-order approximation that enhances formal simplicity.⁷ A_i is the rate constant for the process: it is being assumed to be time-independent for the sake of simplicity. These two simplifying assumptions, linear dependence of the various rates on the x_i and the time-independence of the various rate constants will be made throughout this section and the next. Q_i is a quality factor with value between 0 and 1 that determine what fraction of the x_i catalyzed consists of accurate copies. The second term represents the formation of x_i due to errors in the autocatalysis of molecules of other types: $\phi_{ij} x_j$ is the number of x_j that formed x_i by erroneous catalysis. Similarly, RD_i is assumed to be of the form $D_i x_i$. Finally, emigration of all molecular types from V is assumed to be the same linear function of their respective numbers, that is, RE_i is equal to $E x_i$. With these assumptions, Equation 1 becomes:

$$(dx_i(t)/dt) = (A_i Q_i - D_i - E) x_i + \sum_{j \neq i} \phi_{ij} x_j \quad (\text{Equation 2})$$

(for $i = 1, 2, \dots, N$). Selection occurs in such a system under a variety of conditions that constrain its evolution. The constraint imposed here will be that the population in V remains constant, that is, n is a constant.⁸ This constraint makes the system of differential equations represented by Equation 2 non-linear. A general solution of that system consists of:

$$x_i(t) = n(e_i(t) / (\int_{\alpha, t} ((\sum_k ((A_k - D_k)(x_k(t')/x_j(t')))) e_i(t') dt')) e_i(t)) \quad (\text{Equation 3})$$

$$\text{where } e_i(t) = \exp(\int_{\alpha, t} (A_i Q_i - D_i + \sum_{j \neq i} (\phi_{ij} x_j(t')/x_j(t')) dt') \quad (\text{Equation 4})$$

(for $i = 1, 2, \dots, N$), and the lower limit of integration, α , is determined by initial conditions. Construct the matrix $M_{ij} = (A_j Q_j - D_j) \delta_{ij} + \phi_{ij} (1 - \delta_{ij})$ where $\delta_{ij} = 1$ if $i = j$ and 0 if not. If M_{ij} is non-singular and has no degenerate eigenvalues, then the solution can be written in the closed form:

$$x_i(t) = n((\sum_j C_j q_{ij} \exp(\lambda_j t)) / (\sum_j E_j C_j q_{ij} \exp(\lambda_j t))) \quad (\text{Equation 5})$$

(for $i = 1, 2, \dots, N$), where q_{ij} is the i -th component of the eigenvector corresponding to the eigenvalue, λ_j , of M_{ij} and the C_j are determined by the initial conditions.⁹

An examination of this solution shows that the molecular species with the largest value for $A_i Q_i - D_i$ among those present, will dominate the population provided that the ϕ_{ij} are small. However, the other species will not completely die out and, further, a first-order perturbation treatment shows that, to first order, their numbers will be proportional to the ϕ_{ij} (where the i -th species is the dominant one and the index, j , refers to the other species) (Thompson and McBride 1974). Further, if, due to a mutation (that is, incorrect catalysis), a new type with an even higher value of $A_i Q_i - D_i$ is formed, it will eventually come to dominate the population. This means that, ultimately, the molecular type with the highest possible value of $A_i Q_i - D_i$ will dominate the population. It is easily shown, now, that this system satisfies Lewontin's three criteria for evolution by natural selection. The Criterion of Phenotypic Variation is satisfied because there are different molecular types in the population and because, since not all the Q_i are equal to 1, new types may be created from old ones. The criterion of Differential Fitness is satisfied because the molecular type with the highest value of $A_i Q_i - D_i$ will dominate and the proportion of the others will be determined by the rate at which they may be formed from this one. The Criterion of Heritability of Fitness is also trivially satisfied because, in general, each molecule catalyzes the formation of another of its own type.

4. Complementary Replication with Natural Selection

Systems with complementary replication are those in which one polymer type catalyzes the formation of a second which, in turn, catalyzes the formation of the first. Such systems are particularly interesting because this is the mode of replication in contemporary

DNA and presumably was so in primordial RNA if, indeed, RNA was the original carrier of genetic information. In such a system the rate of production of a molecular type is a function of the number of molecules of its complement. A model of such a system can be represented using the same notation as in Section 3. However, a slight change makes the properties of such systems much more perspicuous. Let σ take the values +1 or -1. Let the subscript σ, i characterize parameters corresponding to the molecular type complementary to those characterized by $-\sigma, i$. Other than this difference in the subscripts, let A, Q, D, E (which has no subscripts) and ϕ have the same form and interpretation as in Section 3. Given these assumptions and this notation, for this model, Equation 1 becomes:

$$(dx_{\sigma, i}(t)/dt) = A_{\sigma, i}Q_{\sigma, i}x_{-\sigma, i} - (D_{\sigma, i} - E)x_{\sigma, i} + \sum_{j \neq i} \sum_{\sigma' = +1, -1} \phi_{\sigma, i; \sigma', j} x_{\sigma', j} \quad (\text{Equation 6})$$

(for $\sigma = +1, -1; i = 1, 2, \dots, N$). This represents a system of linear differential equations just like Equation 2 with one difference: now there are $2N$ equations rather than N . Non-linearity is introduced here, as in Section 3, by the selection constraint that the total population remains constant.

Formally, therefore, the system represented by Equation 6 is the same as that represented by Equation 2 and can be analyzed in exactly the same way. If the following simplifying assumptions are made about the relations between each molecular type and its complement, then some particularly simple conclusions can be drawn (Thompson and McBride 1974). *First*, it is assumed that the production rate is the same for complementary types, that is $A_{\sigma, i} = A_{-\sigma, i} = A_i$. This is reasonable, for instance, if molecules of complementary types serve as physical templates for the formation of each other. *Second*, it is assumed that the quality factor is the same for complementary types, that is, $Q_{\sigma, i} = Q_{-\sigma, i} = Q_i$. Once again, this is reasonable for template-directed replication because the production of either complement involves the same physical process. *Third*, it is assumed that the decay rate is the same for complementary types, that is, $D_{\sigma, i} = D_{-\sigma, i} = D_i$. This is reasonable, for instance, for all polymers with identical bonds between sub-units if decay occurs by the disruption of such bonds. Given these assumptions it can be shown that the number of the molecules of each type is a monotonically increasing function of $A_i Q_i / D_i$ provided that mutation rates are small. The relative numbers of other types ultimately present depends on the mutation rates as in the model discussed in Section 3. This model satisfies Lewontin's criteria for exactly the same reasons the last one did.

5. Hypercycles and the Origin of Life

The complementary replication model just discussed can be considered as a catalytic cyclic reaction process involving just two molecular types (see Figure 1a). Similarly, there can be such cyclic processes with m members where each type x_i catalyzes x_{i+1} for $i = 1, 2, \dots, m$ and x_m catalyzes x_1 (see Figure 1b). If at least one R^B_i in a cyclic process is of higher order than 1 in the x_i 's, then the system is called a hypercycle.¹⁰ Hypercycles can be of several types. A m -member hypercycle is *simple* if: (i) for each i , R^B_i depends on x_i (giving rise to partial autocatalysis); (ii) each R^B_i is a homogeneous polynomial of the k -th degree of the x_i 's ($k \leq m$); (iii) any x_i (of the members of the hypercycle in question) occurs only to first order, if at all, in any R^B_i (see Figure 2). In a *catalytic* hypercycle, some of the R^B_i need not contain x_i . The last situation holds, for instance, when some of the members cannot catalyze their own formation. An example of a catalytic hypercycle where nucleic acids reproduce by complementary replication and also code for proteins which catalyze the former reaction (and others) is shown in Figure 3.

Phenomenological equations (represented by Equation 1) can be constructed for hypercycles. Eigen and co-workers have shown, by computer simulations (these systems are almost always too complicated for analytic solution) for a variety of situations that



Figure 1: (a) A 2-member cyclic reaction like the complementary replication model discussed in Section 4; (b) an n -number cyclic reaction. If the formation rate term is non-linear, either cycle is a hypercycle.

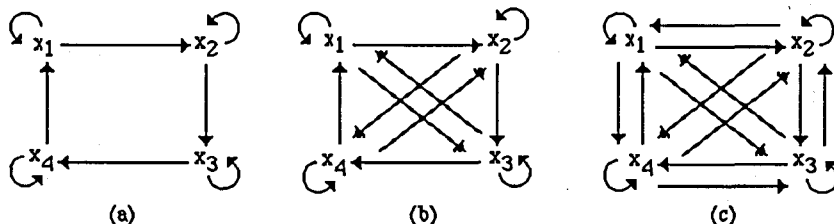


Figure 2: A 4-member simple hypercycle. (a) Degree = 2. $R^B_1 = A_1 Q_1 x_1 x_4$, $R^B_2 = A_2 Q_2 x_2 x_1$, etc.; (b) Degree = 3. $R^B_1 = A_1 Q_1 x_1 x_4 x_3$, $R^B_2 = A_2 Q_2 x_2 x_1 x_4$, etc.; (c) Degree = 4. $R^B_1 = A_1 Q_1 x_1 x_4 x_3 x_2$, $R^B_2 = A_2 Q_2 x_2 x_1 x_4 x_3$; etc.

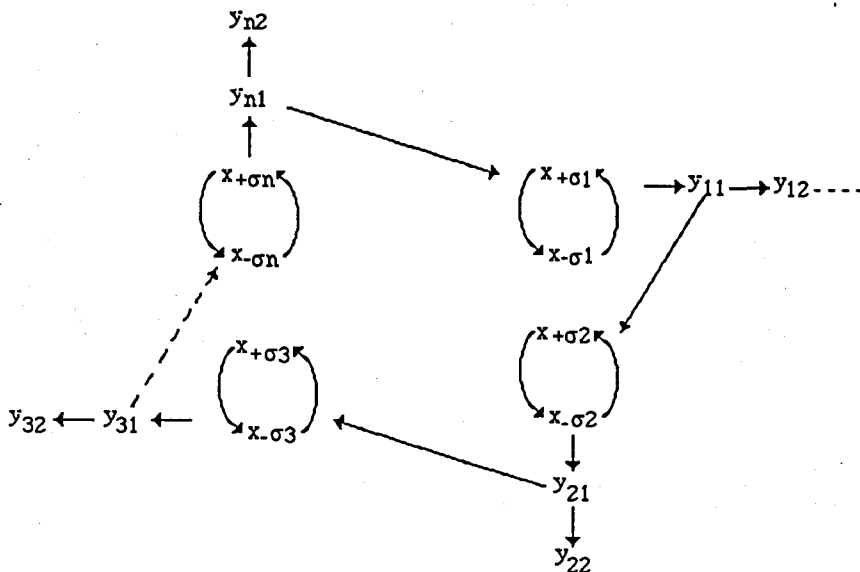


Figure 3: A catalytic hypercycle. The x_{σ_i} - $x_{-\sigma_i}$ pairs represent nucleic acids undergoing complementary replication. The x_{σ_i} - $x_{-\sigma_i}$ nucleic acids code for a protein y_{i1} which catalyzes the replication of the $x_{\sigma_{i+1}}$ - $x_{-\sigma_{i+1}}$, etc. The proteins can also catalyze other proteins in chain reactions $y_{ij} \rightarrow y_{i,j+1} \rightarrow y_{i,j+2}$, etc. Such a hypercycle represents, in highly simplified and idealized form, the type of protein-nucleic acid coupling in living systems. Such a hypercycle, in the pre-biotic environment, according to the Eigen theory, is the most likely candidate for the origin of life.

"once-for-all" selection occurs in such systems: the hypercycle type selected undergoes hyperbolic growth and all other types rapidly become negligible. Such a system presents an interesting model for the origin of life on earth for two reasons: (i) it can incorporate protein-nucleic acid coupling; and (ii), most importantly, it explains the universality of the genetic code: the genetic code that exists today is simply the one incorporated in the hypercycle selected in prebiotic time.¹¹

6. Functional Explanation in Molecular Biology: DNA and RNA

The ability to provide a physical explanation of evolution by natural selection becomes particularly important when attempts are made to provide a physical warrant for functional explanations in molecular biology. A characteristic example of such explanations, originally invoked by Rosenberg (1985, pp. 38 -43), is the following.¹² In virtually all living organisms there is a difference between DNA and RNA. Whereas DNA consists of the nucleotide of the four base types adenine (A), cytosine (C), guanine (G), and thymine (T), RNA consists of A, C, G, and uracil (U) instead of T. The question that arises is the source of this difference. It does not alter the coding properties of either of the acids. U is so structurally similar to T that the possible structural roles are also unaltered. Further, T is synthesized from a uracil deoxyribonucleotide by an endothermic reaction. That suggests that whereas energetic considerations might partly account for the occurrence of U in RNA, they cannot account for the occurrence of T in DNA.

The provisional explanation of this difference between DNA and RNA is somewhat complicated. C in DNA can easily convert to U by deamination. When this occurs, the coding property of a DNA chain is destroyed because of the presence of a foreign base type, U. However, such a situation almost never pertains in a living cell because of the presence of a number of enzymes which, through a complicated process, remove U from DNA and replace it with C. Had U ordinarily occurred in DNA, this repair mechanism would be completely ineffective since it would excise a normal base type from DNA and replace it with something else. Further, in the absence of any repair mechanism, the code contained in the DNA chain would be quite unstable because not all C→U mutations are silent. Thus, the incorporation of T in DNA instead of U enhances the stability of the code contained in a DNA chain which more than makes up for the additional energy expenditure. Now DNA, as the genetic material, has a long existence (of the order of the lifetime of the individual) during which a stable code needs to be maintained, whereas RNA has a relatively short life (of the order of the time it takes for translation at the ribosome). In the case of RNA, therefore, stability of the code is not so important, and is not worth the additional energy expenditure. An explanation of this kind is a functional explanation.¹³ T occurs in DNA because it is the function of DNA to carry a stable code over long periods of time and it is a function of T to enhance this stability of the code. No similar functional role could be assigned to T had it occurred in RNA.

In order to guarantee the adequacy of the explanation offered two separate conditions must be satisfied, and this is generally true of functional explanations in molecular biology. *First*, the various factors that were adduced must be known to be empirically true. It will be assumed here that they are; some reservations will be noted in Section 8. *Second*, and much more important, it must be shown that the explanation is causal and, on the surface, there seems to be at least one good reason to doubt that it is: it invoked a consequence of the incorporation of T in DNA rather than antecedent factors. The last problem is resolved by invoking true "function statements" of the form: "According to theory *T*, a function of feature *x*, in having property *Y*, in system *S*, in environment *E* relative to purpose *P* is to bring about consequence *C*" (Wimsatt 1972, p. 32). "*T* is a causal theory that requires that if *x* has *Y* in *S* in *E*, *C* obtains. Some other causal theory, *T'*, normally an explicit selection theory, specifies what constitutes a purpose and when a function statement is true. Since both these theories are causal and function-statements hold antecedent to the result in question actually occurring, the explanations become causal. In the example being discussed, *x*

is the occurrence of T in DNA; Y is the ability of T to resist excision by the mechanisms that replace U with C; S is a DNA polymer; E , the environment, contains the various enzymes responsible for the DNA repair discussed above; P is the stability of the DNA sequence; and C is that repair of DNA. T is simply the chemical theory that specifies the various interactions that cause such repair: obviously it is causal. Finally, T' is simply the theory of natural selection at the molecular level applied to systems undergoing complementary replication as modelled in Section 4 with all the simplifying assumptions along with the following definition and stipulation. Define as a "purpose" any property of a molecular type the augmentation of which increases its rate of growth relative to other types, all other factors remaining constant.¹⁴ Next, stipulate that, a function statement is true if C causes the system to have some such property. T' is evidently causal since the theory in Section 4 was manifestly developed as a causal theory and the addition of this definition and stipulation does not alter that. Given these considerations, if it can now be shown that the function statement obtained after these specifications is true, the functional explanation under question will have been shown to be adequate. It is obvious that C causes S to have P . What remains to be shown is that P satisfies the definition of a purpose and it suffices to do this using any of the laws adduced in T' . In order to avoid repetition this is only done in the next section where it is simultaneously shown that the truth of that function statement can be guaranteed on purely physical grounds.

7. A Tentative Physical Warrant for a Functional Explanation

The causal adequacy of a functional explanation does not imply, of course, that this adequacy can be guaranteed on purely physical grounds. In order to accomplish the latter task two other criteria must be shown to be satisfied. *First*, it must be shown that T and T' are theories that are true for purely physical reasons. *Second*, it must be shown that the truth of the function statement being invoked can be certified on purely physical grounds. In the example being discussed here T is simply the theory of chemical interactions that are responsible for DNA repair, and these obviously occur because of physical law. T' is the theory of selection at the molecular level as noted and augmented in Section 6. This was manifestly constructed using not only causal, but only physical, assumptions. Thus the first criterion is trivially satisfied.

In order to satisfy the second criterion, it first needs to be shown that P satisfies the definition of a purpose on purely physical grounds. In order to do this, assume, *first*, that S , one DNA polymer reproducing by complementary replication competes with a pair of complementary RNA polymers. *Second*, assume that E is the environment specified in Section 6, that is, it contains some set of molecules that excise U from DNA and replace it with C and further require that no similar repair mechanism exists for RNA. *Third*, assume that $A_{DNA} = A_{RNA}$ and $D_{DNA} = D_{RNA}$. Now $Q_{DNA} > Q_{RNA}$ because random deamination causes the number of molecules of the RNA type to decrease by converting to new types during the course of replication. Hence $A_{DNA}Q_{DNA} - D_{DNA} > A_{RNA}Q_{RNA} - D_{RNA}$. Using the conclusions of Section 4, the DNA pair will grow more rapidly than the RNA. Thus the greater stability of the DNA sequence causes the DNA polymer to grow more rapidly than the RNA polymers present. In other words, P satisfies the definition of a purpose on purely physical grounds.¹⁵ That C causes S to have P is also true on physical grounds: in fact, it is trivially true because DNA repair physically ensures that the DNA sequence is stable. Hence the second condition is also satisfied.

8. Conclusion

The purposes of this paper were, *first*, to show that a physical theory of natural selection at the molecular level could be developed for a variety of systems of which that consisting of hypercycles is just one and, *second*, to show that this theory can be used to provide physical warrants for functional explanations in molecular biology. The first purpose has been successfully achieved.¹⁶ Some reservations, however, need to be expressed

about the success of the achievement of the second though, if the discussion in Sections 6 and 7 has any merit, some success has indeed been achieved. *First*, it has been assumed without argument that the DNA-RNA example is typical. However, there is one good reason to make this assumption: no functional argument in molecular biology that does not fit this pattern has yet gained prevalence in the literature.¹⁷ *Second*, and more important, all three assumptions about the DNA-RNA competition made in Section 7 are open to question on empirical grounds. In particular, the assumption that the DNA repair mechanism, that plays such a crucial role there, existed in the prebiotic environment or only shortly afterwards is problematic though there is yet no evidence either way. Further, the assumption that there was an isolated region on earth in which primitive systems, of both DNA and RNA, reproduced themselves by complementary replication, might also be inadequate. On the other hand, if one or more of these assumptions is false, it might be the case that the functional explanation in question is itself incorrect: the correctness of functional explanations is proverbially difficult to gauge. As far as functional explanations go, all that this paper does, perhaps, is to show the *type* of argument that would be necessary to provide physical warrants for them. To the extent that the second purpose is achieved, this paper furthers the program of explanatory reductionism in molecular biology, that is, the program of showing that all phenomena in molecular biology can be explained on physical grounds. As far as that program is concerned this paper also achieves another end that is of some interest to it: from a physical scientist's point of view it demystifies both evolution by natural selection and functional explanation.

Notes

¹Thanks are due to William C. Wimsatt for comments on an earlier draft of this paper.

²Eigen (1971) is the source of these developments; the most complete accounts of the developments so far achieved are Eigen and Schuster (1979) and Küppers (1983).

³For a penetrating discussion of some of the most important objections to the Eigen theory of the origin of life, see Dyson (1985), Chapter 2.

⁴By "explanatory reductionism" is meant the explanation of upper-level phenomena (not necessarily laws) by means of phenomena and mechanisms at a lower level. For the distinctions between "theory," "explanatory" and "constitutive reductionisms," see Mayr (1982), pp. 59-63 and Sarkar (1988).

⁵The assumption of equal length for all polymers in the population is made for simplicity. It can be disposed of with no loss of generality for the conclusions reached here.

⁶Note that since V is constant the x_i can also be regarded as concentrations.

⁷This assumption would be true if, for instance, each molecule served as a physical template for the production of another molecule of the same type.

⁸For a discussion of other constraints that result in selection, see Küppers (1983) and Bernstein, *et. al.* (1983).

⁹For a derivation of Equations 3, 4 and 5, see Sarkar (1988), Chapter 4, and the references therein.

¹⁰Note that the critical property of a hypercycle in this definition is the non-linear dependence of the formation rate terms on the x_i 's and *not* the coupling together of different cycles. No precise definition of a hypercycle has yet been offered by Eigen and his co-workers! The one adopted here seems to capture the spirit of the discussion in Küppers (1983) where the description closest to a definition is found.

¹¹See Dyson (1985) for a critical estimate of this model for the origin of life.

¹²For more details of this example, and for other examples of functional explanations in molecular biology, see Sarkar (1987).

¹³The account of functional explanation used here is due to Wimsatt (1972); for a defence of this approach in the general context of functional explanation in molecular biology see Sarkar (1987).

¹⁴Note that this definition of "purpose" is consistent with but not identical to that given in Wimsatt (1972). On Wimsatt's account, many of these properties will be lower order functions.

¹⁵Note, therefore, that it does so on causal grounds, thus showing also that the adequacy of the functional explanation adduced in Section 6 is also guaranteed.

¹⁶It should be emphasized, though, that natural selection occurs at many other levels: the individual, for instance. The considerations adduced here do not, in any immediately suggestive fashion, carry over to those levels.

¹⁷See Sarkar (1988), Chapter 4 for a defence of this claim.

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