will be of special interest to those concerned with philosophical problems closely related to the physical sciences. The problem of "the direction of time" in its various forms and connections receives perhaps the most attention in both volumes, being treated in several excellent papers and review articles. Ontological questions concerning the reality of time and of temporal becoming also receive considerable attention, as do the various philosophical problems and paradoxes associated both with the theory of relativity and with the various field theories of contemporary physics. The methodological problems of time perception and measurement (in physics, biology, and psychology) are also considered in both volumes. Both devote space to differing conceptions of and attitudes toward time. *Time in Science and Philosophy* features the article on time in Indian philosophy already mentioned. *The Study of Time* contains several psychological, sociological, historical, cultural, and philosophical studies of a range of time concepts and their intricate interconnections with other factors, as well as the fascinating and readable selection of articles, also already mentioned, on the disrupting and disorienting effects of long transmeridian flights.

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Neutralists vs. Selectionists

Proceedings of the Sixth Berkeley Symposium on Mathematical Statistics and Probability. Vol. 5, Darwinian, Neo-Darwinian, and Non-Darwinian Evolution. LUCIEN M. LE CAM, JERZY NEYMAN, and ELIZABETH L. SCOTT, Eds. University of California Press, Berkeley, 1972. xvi, 370 pp., illus. $13.50.

Do not be deceived by the title of this book. It contains little about statistics and almost nothing about Darwin. It does, however, give an excellent sample of the recent arguments about molecular evolution, written in a manner intelligible both to biologists and to mathematicians.

The debate has been heated, and there has been a tendency for each side to ignore the arguments of the other. The issues have become clouded rather than clarified. The book is therefore particularly valuable for allowing us directly to compare the different points of view.

The comparison is not very flattering to either party, and the reader may be forgiven if occasionally he throws down the book in disgust and says "a plague on both your houses."

Yet the issues are important, theoretically and practically. Has the greater part of our evolution been the result of random substitutions, effectively neutral in selective value? Are the many enzyme polymorphisms in human populations merely "evolutionary noise"? If they are not, they must affect—or have affected—our survival or reproduction. These are matters of concern.

Even in matters of concern it is depressing how easily myths and misconceptions can become accepted as scientific truths. Once they get embedded in the literature, it is difficult indeed to winkle them out. Nonetheless the attempt must be made.

I will start with a personal but illustrative example. In 1957 Dobzhansky and Pavlovsky published an experiment purporting to show the interaction between random genetic drift and natural selection. Shortly thereafter, Williamson and I published in the same journal a note pointing out (albeit timidly, for we were young then and Dobzhansky was already a great man) that their data appeared to be clumped, that their statistical test was therefore inappropriate, and that their results seemed to be statistically insignificant. We were correct but, from that time to this, Dobzhansky and Pavlovsky's paper has been quoted without qualification in virtually every textbook of population genetics and nearly every discussion of genetic drift. It appears again in Crow's introduction to this symposium, quoted with approval and without reserve.

There are more serious cases. A new and popular misconception is that, for individual classes of proteins, evolutionary rates are constant. Kimura and Ohta's contribution to the book makes much of this "constancy" despite the fact that their own data show significant variations between different lines of descent, and despite the fact that the averages within lines are calculated for such long periods that the differences between them would permit very large changes of rate (even by orders of magnitude) over shorter intervals. Kohne *et al.*, in another paper, report that the rates of evolution in nonrepetitive DNA are variable and appear to be related to generation time. Nevertheless Jukes, in the same book, baldly states that "the evolutionary clock ticks slowly in proteins, independent of speciation, generation time or gene duplication." After this, he goes on to accuse the selectionists of fitting all molecular changes in evolution to "the Procrustean bed of pan-selectionism."

Three papers (by Crow, Kimura and Ohta, and King) reproduce a neat example of circular reasoning. Each of them expresses pleasurable surprise that Fitch's "covarions," studied in cytochrome c, hemoglobin α and β chains, and fibrinopeptide A, seem to evolve at nearly equal rates. These covarions were postulated following Fitch's attempt to define two exclusive types of sites within proteins (variable and invariant). When it became apparent that the data were not consistent with this dichotomy, the concept was refined to include the hypothesis that the array of variable sites (covarions) changes with time. Disregarding the doubtful business of imposing a system of strict alternatives on variation that is clearly continuous, it is important to recognize that slowly evolving proteins are supposed to have relatively fewer covarions and faster-evolving proteins are supposed to have relatively more. The inevitable result of this arrangement is that the evolutionary rates of the covarions will be much more alike than the rates of the proteins themselves. Their similarities should be no source of surprise, and cannot be construed as evidence of neutrality, or of anything else.

Another popular misconception, pointed out by Stebbins and Lewontin in a thoughtful essay, is the "fallacy of omniscience"—the assumption that if we cannot immediately see the function of an organic system it is therefore functionless. This fallacy has raised its muddled head many times during the development of evolutionary theory. Newly discovered genetic variation is immediately hailed as neutral, a view that persists for a length of time directly correlated with the degree of our ignorance. This has happened for industrial melanism, for mimicry, for nonmimetic color polymorphisms, and now for enzyme polymorphisms.

The newest candidate is variation in DNA, as shown by the following quotation from Jukes: "Changes in the third base of codons for amino acids will in most cases not produce a change in the amino acid assignment, so that in such cases they are, therefore, selectively neutral." This assertion not only manifests the fallacy of omniscience, it also ignores a good deal of evidence that natural selection can act directly on the composition of nucleic acids.

By rigorously following the "neutralist" argument, Kimura and Ohta have maneuvered themselves into the entertaining position of having to postulate that the majority of the changes during evolution have been mildly deleterious. The concept of evolution taking place against a background of progressive deterioration is one whose implications remain to be explored. Does it predict, for example, that life could not indefinitely survive in a perfectly constant environment? We must await the answers with impatience.

If, in this book, the arguments for neutrality leave something to be desired, so alas do the arguments for selection. Ayala, for example, claims that the relative uniformity of the numbers of alleles and their frequencies among widely separated natural populations of *Drosophila willistoni* are incompatible with neutrality. However, they might well be the result of a recent "bottleneck" in numbers followed by a rapid expansion of range. Similarly, his finding that alleles at the *Lap-5* and *Est-5* loci come to equilibrium in experimental populations does not demonstrate that they are directly subject to selection. It might be due to their being in a state of linkage disequilibrium with selectively important alleles at other loci. This disequilibrium could also be the consequence of a recent constriction in numbers. Explanations in terms of bottlenecks may not be the correct ones, but at least they should be considered.

The conclusions of Allard and Kahler are subject to similar reservations. Several polymorphic loci of the wild oat *Avena barbata* show parallel variations that are correlated with changes of habitat from xeric to mesic. This, however, does not necessarily mean that the loci themselves are subject to selection. Another plausible hypothesis is that there are two distinct genetic entities (semispecies) with different ecological preferences, hybridizing in some habitats. Although *Avena* is largely self-fertilizing, hybridization is common within the genus, and attributions to particular species are often difficult. Allard and Kahler do not discuss these difficulties.

In another paper, Gatlin reports her studies on the "information density" of DNA. She defines a component that measures the degree to which the probability of occurrence of a base depends upon the nature of the adjacent bases. She makes the interesting observation that the value of this component appears to have increased during the evolution of vertebrates. On the basis of her findings, she claims to have discovered a new evolutionary principle, that natural selection acts to improve the informational efficiency of the "source" (DNA). If she is merely proposing that selection acts directly on the DNA, and can improve its efficiency, then her principle is not new. If, however, she is going further, as she seems to be, and claiming that selection acts directly on the characteristic of informational efficiency, then her claim is premature. There are several parameters ($\bar{W}$ for example) that are increased as a result of natural selection, but on which it does not act directly. They are consequences rather than causes.

Reichert adapts Gatlin's methods to the study of proteins, and in the course of his discussion wins this year's Lewontin Prize for the best throwaway remark: "The molecular biological format provides a testable basis for significance, and may even lead us, quite incidentally, to the meaning of meaning."

This indeed would be a desirable destination, but on the way we are faced with the more prosaic matter of attempting to decide whether or not natural selection has been the dominating factor in molecular evolution. How are we to proceed? The two most critical essays in the book, by Stebbins and Lewontin and by Bodmer and Cavalli-Sforza, make it clear that juggling with numbers will not solve the problem. Our present estimates of evolutionary rates, mutation rates, genetic loads, effective population sizes, and numbers of genes are all so inexact that by a suitable choice of values we can favor either case. Clearly these estimates must be refined, but there are other approaches. The most obvious, and in my opinion the most likely to be productive, is to study the properties of the molecules themselves, to discover if contemporary variants of enzymes differ in their biochemical activities, and to find out if the differences are detectable by natural selection. The task is not easy, but the first steps have been taken. A fascinating example is provided here by MacIntyre, who reports an inquiry into the differences between the homologous enzymes of closely related species, using the techniques of subunit hybridization. The results of this study leave little doubt that the differences have important biochemical effects. They provide little comfort for supporters of the neutralist view.

It is surprising that none of the contributors has clearly made the most obvious point about molecular evolution. While the arguments for neutrality are inadequate, and the direct evidence for selection is inconclusive, the selectionist hypothesis remains the most economical one. A large part of biological research during the past century has been involved in establishing the primary role of natural selection. It would be illogical to change course, in the face of all the evidence, because of a temporary ignorance.

In whatever way the debate may eventually be resolved, at the present we must content ourselves with the fare that is offered by this book. It contains some good meaty pieces of reading and much entertainment, both intentional and unintentional. It can be recommended to believers and cynics alike, but while digesting it they are cautioned to remember the prescient words of Goethe: "The web of this world is woven of Necessity and Chance. Woe to him who has accustomed himself to finding something capricious in what is necessary, and to ascribe something like reason to what is capricious."

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A Sampling of Ecology

Growth by Intussusception. Ecological Essays in Honor of G. Evelyn Hutchinson. E. S. DEEVEY, Ed. Connecticut Academy of Arts and Sciences, New Haven, 1972 (available from Archon Books, Hamden, Conn.). 442 pp. + plates. Paper, $25. *Transactions* of the Academy, vol. 44, Dec. 1972.

The title of this volume may conceivably mislead some medically oriented readers. This bit of mystification, chosen by the editor, is something