Evolving Genes and Proteins

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Degeneracy of the Genetic Code: Extent, Nature, and Genetic Implications

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SUMMARY

Part I of this paper deals with the amount of degeneracy in the genetic code or, looked at in reverse, the amount of nonsense. Section A considers the experimental evidence and suggests (a) that technical difficulties have prevented assigning meaning to the still unassigned triplets and (b) that the validity of the earlier evidences for nonsense triplets may be questioned in the light of recent discoveries. Complete degeneracy of the code and total absence of nonsense have not yet been excluded. Section B comes to the conclusion, on the basis of general evolutionary considerations, that natural selection would be expected to establish and preserve a completely degenerate code. Section C points out that different nondegenerate codes differ greatly in the builtin frequency of nonsense mutations by single base substitutions.

Part II deals with the nature of degeneracy in the existing code. The high frequency of

Part II deals with the nature of degeneracy in the existing code. The high frequency of shared doublets between â€œsynonymsâ€ (i.e., codons for the same amino acid) suggests that they are â€œconnected,â€ that is, interconvertible by altering one base only. Among the sets of synonyms thus far reported, some must be completely connected, and, in the absence of knowledge of the order of the bases, the synonyms of each set could be ordered so as to be completely connected. Current knowledge leads to the expectation of either complete connectedness or a high degree of connectedness among synonyms.

Part III explores the consequences of complete connectedness between synonyms; the consequences would be modified only quantitatively, not qualitatively, if connectedness is less than complete. Section A discusses â€œsilentâ€ mutations, i.e., single-base changes that yield a synonym. These must occur in the code as now known. Their frequency (if equal probability of all base substitutions is assumed) depends on the number of synonyms in a set, on the way in which the synonyms are connected, and on whether the various synonyms are used equally or unequally. By selecting one synonym of a set for almost exclusive usage, the minimal percentage of silent mutations stays constant at 11.1% in sets of two or more synonyms, but the maximum increases steadily with set size up to 100% in sets of ten or more. If the synonyms of a set are equally used, the pattern of connection that yields the highest frequency of silent mutations gives peaks for sets of four, seven, and ten synonyms. It would not be surprising if 20% or more of all single-base mutations were silent unless the frequency of trans versions is greatly restricted. Comparable analyses can be made of a quadruplet code. The frequency of mutations to synonyms is not enough to account fully for modulatory mutations, but it is enough to constitute a potential source of error in certain amino acid replacement studies. Section B points out that the degeneracy of the existing code implies as an evolutionary consequence a molecular orthogenesis, that is, marked built-in differences among the synonyms of a set in their possible amino acid replacements by single-base mutations. Section C shows the surprising fact that crossing over between synonyms must in certain cases yield recombinant codons for a different amino acid. Although likely to be scored as mutations, these recombinations would be much more frequent than true mutations. The advantage of connected synonymy is opposed by the disadvantage of these recombinational pseudomutations. Possible ways out of this paradox are discussed.

1 Publication No. 759 from the Department of Zoology, Indiana University. At the Symposium, only Part III of this paper was presented, and in very abbreviated form, because of the lateness of the hour. I thank the editors for permitting and encouraging me to include the full paper in the printed record. This work was supported by Contract COO-235-15 of the Atomic Energy Commission and Grant E81G of the American Cancer Society.

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