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REVIEW ARTICLE

THREE-DIMENSIONAL MODEL OF THE GENETIC CODE

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Abstract

The classical table of the genetic code does not reflect all the relations among the codons. This paper demonstrates that the three-dimensional topological model — cube enveloping a sphere — is the source of all the relations within the genetic code: eight cognate codons, disposed at the corners, make up the main cube; then, according to the superposition principle, these eight cubes make up a bigger (common) cube containing all the 64 codons. The topological relation between the cube and the sphere inscribed in the cube is expressed by Euler's theorem of homeomorphic translation. Using this three-dimensional model, a new table and a new matrix of the genetic code can be worked out, representing the relations among encoding words (codons), in the actual DNA and RNA molecules far more precisely than the classical ones.

Introduction

In spite of its adequate name from the very beginning of investigations in molecular biology, the genetic code has not been sufficiently and comprehensively explored as a code, i.e. as a mathematical essence of the relations. This task, however, has been present since 1963, when all the 64 codons were practically known. The fact that the genetic code is in full accordance with the mathematical model for generating three-letter words out of a four-letter alphabet (third class variations with repetition, out of a four-element set 4^3), led to further necessary and evident deductions. So, after 1966, when the genetic code table was finally established, it was necessary to search for a solution of the obvious problem of two sites in the table being „occupied” by serine and two by arginine. The main purpose of both the previous (Rakočević, 1988a; 1988b) and this work was actually that necessary deduction, based on appropriate theoretical and experimental data.

The whole project has proved to make sense, since it has led to a significant result, which may be summarized as follows:

The genetic code, as a unity of a nucleotide and an amino acid component (the encoding words and encoded elements from the first and the second alphabet, respectively) is in full accordance with the three-dimensional topological model of a cube with an inscribed sphere, their mutual relation being described by Euler's theorem of homeomorphic translation. The degree of difference between codons (which occupy the cube corners on the topological model) corresponds precisely to mutual distances between the corners: 1 step (or 1 bit in the binary record) if the codons are at opposite ends of the edges; 2 steps, if they are at opposite ends of face diagonals, and 3 steps if they are at opposite ends of the cube diagonals. In the matrix of distances between the codons (Table 1), which is derived directly from this three-dimensional model, zeros are consistently situated on the diagonal (one does not differ from itself), while unities follow as the next number sequence along the diagonal. They testify to the optimum ¹ quality of the genetic code revealed in the regular one-unit distance between adjacent codons, according to similarity-dissimilarity criterium.

al
H

Table 1. The optimal distance matrix for 20 protein amino acids.

	F	L	I	M	V	T	A	P	S	G	N	K	D	E	R	C	W	Y	H	Q
F	0	1	1	1	1	2	2	1	1	3	2	2	2	2	2	2	2	1	1	1
L	1	0	1	1	1	2	2	1	1	3	2	2	2	2	2	2	2	1	1	1
I	1	1	0	1	1	1	1	2	2	2	1	1	1	1	2	3	3	2	2	2
M	1	1	1	0	1	1	1	2	2	2	1	1	1	1	2	3	3	2	2	2
V	1	1	1	1	0	1	1	2	2	2	1	1	1	1	2	3	3	2	2	2
T	2	2	1	1	1	0	1	1	1	1	2	2	2	2	1	2	2	3	3	3
A	2	2	1	1	1	1	0	1	1	1	2	2	2	2	1	2	2	3	3	3
P	1	1	2	2	2	1	1	0	1	2	3	3	3	3	1	1	1	2	2	2
S	1	1	2	2	2	1	1	1	0	1	1	1	1	1	1	1	1	2	2	2
G	3	3	2	2	2	1	1	2	1	0	1	1	1	1	1	1	1	2	2	2
N	2	2	1	1	1	2	2	3	1	1	0	1	1	1	1	2	2	1	1	1
K	2	2	1	1	1	2	2	3	1	1	1	0	1	1	1	2	2	1	1	1
D	2	2	1	1	1	2	2	3	1	1	1	1	0	1	1	2	2	1	1	1
E	2	2	1	1	1	2	2	3	1	1	1	1	1	0	1	2	2	1	1	1
R	2	2	2	2	2	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
C	2	2	3	3	3	2	2	1	1	1	2	2	2	2	1	0	1	1	1	1
W	2	2	3	3	3	2	2	1	1	1	2	2	2	2	1	1	0	1	1	1
Y	1	1	2	2	2	3	3	2	2	2	1	1	1	1	1	1	0	1	1	1
H	1	1	2	2	2	3	3	2	2	2	1	1	1	1	1	1	1	0	1	1
Q	1	1	2	2	2	3	3	2	2	2	1	1	1	1	1	1	1	1	1	0

Review of historical background of the genetic code

The fact that extremely abundant experimental data were, from the very beginning, followed by profound theoretical generalizations, is very important for the development of genetic code theory. If we take the year 1944, as the actual starting point, when the important discovery, demonstrating that nucleic acids, not proteins, represent the chemical basis of genes, was made (Avery *et al.*, 1944), we can say that theory preceded experiment. As early as in February 1943, Erwin Schrödinger of the Trinity College, Dublin presented a lecture entitled „What is life?”, with „chromosome fibre” playing the central part. The very next year, i.e. the starting year of molecular biology, Schrödinger published a book (Schrödinger, 1944) with the same title, where he set forth the idea that the chromosomes contain in some kind of code-script the entire pattern of the individual's development.

These two events will, in my opinion, prove to be the key events in paving the way for the investigations of the essence of the genetic code. What will also turn out to be true, however, is that theory has been lagging behind in the course of further development of molecular biology; even now it is difficult to cope with the innumerable experimental data. A comprehensive and more complete theory of the genetic code is still missing.

In order to be able to grasp the keystone point in which (or, to be more precise, from which) genetic code theory could not keep abreast, we shall set forth the major steps in the investigations since 1944.

In 1950, Chargaff discovered certain regularities in the structure of the deoxyribonucleic acid, DNA (Chargaff, 1950); the total amount of purine nucleotides in a DNA molecule is equal to the amount of pyrimidine nucleotides; the molar ratio A/T, as well as G/C, is 1. Two years later, it was conclusively established that nucleic acids were really the chemical basis of heredity (Hershey and Chase, 1952); this was established on a material different from that on which Avery's group worked (Avery, 1944).

On the basis of these results, as well as on the remarkably well done Wilkins' DNA X-ray studies (Wilkins, 1953), it was possible to obtain the most important discovery in molecular biology — the discovery of the „double helix” to decipher the DNA structure (Watson and Crick, 1953).

Running parallel to the investigations of the chemistry and structure of nucleic acids, there were investigations which demonstrated that nucleic acids played an important part in protein biosynthesis (Cf. Caspersson, 1941; Brachet, 1947; Moldave, 1965; Novelli, 1967) and that the whole process occurs on ribosomes (Cf. Zamecnik, 1956 and 1960). On the basis of all these results, a *code hypothesis*, according to which only a small number of DNA molecular units take part in amino acid decoding during the formation of a polypeptide chain, was inevitable. But how many of these units are included? Gramow (1954) demonstrated that — for mathematical reasons — it followed axiomatically that the nucleotide encoding words (codons), in the encoding process of the 20 amino acids, must be triplets. The first experimental proofs of this

were obtained by Nirenberg and Matthaei as early as 1961 (Nirenberg and Matthaei, 1961). The existence of all the 64 codons was experimentally established between 1961 and 1964. (Nirenberg, et al., 1963; Ochoa et al., 1964; Matthaei, et al., 1962).

In future, upon thorough studies of the „logic” of all these experimental discoveries, I believe that this theory will prove to have had a very significant, even decisive, role. Over that period, the crucial role in the formation of the theory was played by Crick, who put forward his „adaptor hypothesis” in 1957, according to which a stereochemical contact between amino acids and the (then only hypothetical) nucleotide triplets was necessary (Crick, 1957). A year later, Hoagland and his co-workers demonstrated that transfer RNA could be such a specific adaptor (Hoagland et al., 1958). Crick’s hypothesis of the „comma-free code” (Crick et al., 1957) is of equal importance. On the basis of these two hypotheses and the general knowledge in the field at the time, (Crick et al., 1961) were able to formulate the theory of the „general nature of the genetic code for proteins”.

The International Symposium on Genetic Code, held in New York, 1966 (Cold Spring Harbor Symposia on Quantitative Biology), was the final achievement in the great synthesis of theory and practice, crowned with the *genetic code table* (Crick, 1966), which has found its way into all textbooks on genetics, molecular biology and biochemistry. Besides Crick, (1966) Morgan et. al., (1967) certainly made a significant contribution towards the composition of this table.

The three-dimensional model — preliminaries

The first significant idea on the steric configuration of the genetic code, i.e. three-dimensional genetic code, was suggested by Eigen and Schuster, later published in a separate study entitled „The Hypercycle” (Eigen and Schuster, 1978). Trying to solve the problem of amino acid distribution in proteins (with regard to the genetic code evolution), they drew up a three-dimensional „table” of the genetic code, in the form of a big cube, accommodating all the codons. The ordering of bases is the reverse of their usual sequence — G, A, C, U — whereby the codons encoding the most widespread amino acids are placed at the very top of the cube. The ingenuity of this idea is remarkable, but its keystone will turn out to be a strict and very exact requirement set by the authors for the construction of the cube: *three coordinates of the three-dimensional geometric space must correspond to the positions of the letters in codon triplets.*

Swanson (1984) started from the same idea in her work from 1984, where she was trying to solve the problem of whether „a unifying concept for the amino acid code” was possible. On the basis of the relevant and valid hypothesis that it is possible to arrange the 20 protein amino acids in such a way as to form a single „Mutation Ring”, fully interpretable analogous to a Gray code, Swanson drew up a „Codon path cube” (Swanson, 1984). She also defined the conditions of further scientific discussion on this scientific problem: „The three edges of the cube represent the three positions in a codon...”; „The relation between the path through the cube and the codon ring is clear if one imagines that codons are strung ... through the cube like beads on a necklace”. The main point of Swanson’s paper is the search for the relations among the codons (hence also of relations among amino acids), mostly in terms of similarity — dissimilarity; still, its greatest value is in the suggestion that these relations cannot be conceived without a three-dimensional model.

In the two previous papers (Rakočević, 1988a; 1988b), it was demonstrated that the three-dimensional model is far more complex. There are at least three levels in the hierarchy of „packing up” the cubes, but the main cube is the one whose eight corners are occupied by eight cognate codons. It is a topological model, so that a homeomorphic translation of the cube into a sphere inscribed in this cube is prerequisite for a full insight into the relations among the codons.

Further considerations (elaborated in this paper) explain these hierarchical relations and demonstrate that the *topological three-dimensional model* of the genetic code is the main source of the most important characteristics of the genetic code, such as the periodic law and the periodic system of the genetic code, the optimum law and the complementarity principle.

The chemical and the mathematical basis of the topological model

First of all, let us consider which experimental data and theoretical propositions suggest that the relations among the codons — and, broadly, all the relations in the genetic code — correspond to the relations in a particular, strictly defined topological model.

It has been experimentally proved that exactly (and only) four specific „small” molecules, uracil (U), cytosine (C), adenine (A), and guanine (G), take part in the composition of tRNA, which mediates transfer of the genetic information. According to theory, there can be exactly 64 three-letter „words”

from this four-letter alphabet, which has been experimentally proved. However, a system of words generated in this way must (axiomatically) have a strictly established regular structure (16 words from the first letter A; 16 words from the second letter A, 16 words from the third letter A, etc.). Hence the question: is not this regularity and symmetry-asymmetry of the codon language a direct outcome of certain regularities of physico-chemical characteristics of the four „small” molecules? Instead of giving a lapidary answer, let us consider the facts: a system of four „small” molecules is made up of two purine and two pyrimidine bases. The molecule from which all the four originate is one and the same — a molecule of pyrimidine. The four of them are mutually distinguishable by three main characteristics: the type of base (purine, Pu, or pyrimidine, Py); the type of functional group in the terminal position (position 6 in purine, position 4 in pyrimidine) — either oxo or amino; and the number of hydrogen bonds linking them in the system codon — anticodon. These three essential characteristics are „distributed” among the four „small” molecules, according to a strict symmetry — antisymmetry rule (Rakočević, 1988a, 1988b). This results in a specific optimum quality: if, out of the four molecules, any two of them are taken, they cannot differ in all of the three essential characteristics, nor can the distinctions be reduced to a single one; whichever two of them are taken, they must differ in exactly (and only) two characteristics! The bases in A.U, i.e. G.C pairs in the codon-anticodon system, do not differ from each other by the number of hydrogen bonds, but they do differ by their base types, and by the functional group in terminal position. On the other hand, however, the functional groups in bases, and these within the base pairs, are „arranged” in the opposite direction: in the first pair, (A,U), the amino group in the terminal position is bound to purine, while in the second pair it is bound to pyrimidine. This symmetry — antisymmetry in the arrangement of functional groups occurs together with the symmetry — antisymmetry of the values for acid-mase constants. So, the relation between pKa values in the first pair is: purine : pyrimidine = 4.15 : 9.5; this is quite reversed (consistently antisymmetrical) in the second pair: purine : pyrimidine = 9.2 : 4.45 (Cf. Rakočević, 1988a).

This leads to the conclusion that any arrangement of letters and words in the codon language is a direct outcome of the regularity in terms of presence/absence of certain physico-chemical characteristics of the molecules of purine and pyrimidine bases. Such an arrangement is also present in a Gray code

model of the genetic code, discovered by Swanson (1984), which, I believe, I have proved to be spatial (three-dimensional), and „functioning” in only one arrangement of (binary recorded) numbers: 7 6 4 5 1 0 2 3 (Rakočević, 1988a).

The main characteristics of the topological model of the genetic code

The essence of genetic code interpretation in the light of the Gray code is in arranging the 64 codons in a circle (to be precise: in the topological space, over the surface of the sphere), in such a way that any two adjacent codons differ at only one letter. If, in a binary record of such an arrangement (Swanson, 1984), a minimization of binary function and form is carried out (Rakočević, 1988a), we shall unconditionally (axiomatically) obtain a situation where the codons from the eight strictly determined groups, occupy positions from the sequence 7 6 4 5 1 0 2 3, alternately (and periodically!).

It is rather easily demonstrable (Rakočević, 1988a, 1988b) that the sequence 7 6 4 5 1 0 2 3 really stands for the sequence of cube corners along the shortest path — along the edges (Table 2). The area of each of the eight codon groups is obtained by topological copying: eight cube corners in six convexly-triangularly bordered areas on the sphere; six faces of the cube into six „corners”, in fact six points of intersection, always including two meridians each (in full accordance with the Euler's theorem; Rakočević, 1988a).

This implies that for a comprehensive interpretation of the relations within the genetic code, a topological model of the cube (codons in its corners) with an inscribed sphere is indispensable and sufficient; the arrangement of spherically curved, triangular areas is also in accordance with the one and only spatial variant of the Gray code model: 7 6 4 5 1 0 2 3.

The logic behind the codon arrangement at cube corners corresponds completely to the logic behind the binary distribution of codons in the binary tree, forming eight-rosette groups (Rakočević, 1988a, 1988b). After the superposition principle, the codons are first arranged in a rosette (following the sequence 7 6 4 5 1 0 2 3, and then the rosettes are „packed” in the same order into a larger rosette. On the cube model, each codon is mounted to a cube corner in such a way that the position of each letter in a triplet corresponds to one of the axes of the three-dimensional co-ordinate system (exactly like Eigen and Schuster (1978) and Swanson (1984) conceived it, albeit not as an element of a complex topological system). Coordinates, i.e. positions in triplets,

Table 2. The new table of the genetic code.

		U	C	G	A	
U [A]	0	UUU	ACU	AGU	AAU	U
	1	UUC	ACC	AGC	AAC	C
	2	UUA	ACA	AGA	AAA	A
	3	UUG	ACG	AGG	AAG	G
C [G]	4	CUU	GCU	CGU	GAU	U
	5	CUC	GCC	CGC	GAC	C
	6	CUA	GCA	CGA	GAA	A
	7	CUG	GCG	CGG	GAG	G
A [U]	0	AUU	UCU	UGU	UAU	U
	1	AUC	UCC	UGC	UAC	C
	2	AUA	UCU	UGA	UAA	A
	3	AUG	UCG	UGG	UAG	G
G [C]	4	GUU	CCU	GGU	CAU	U
	5	GUC	CCC	GGC	CAC	C
	6	GUA	CCA	GGA	CAA	A
	7	GUG	CCG	GGG	CAG	G

* opal

□ ochre and amber

are quantitized: in the *first* position (*x* axis), occupied by the first base in the triplet, the value of that position is 4; in the *second* position (*y* axis), occupied by the second (middle) base in the triplet, the value of the position is 2; the value of the *third* position (*z* axis), occupied by the third base, equals 1. By multiplying (and then adding up) the position values and the binary values of particular bases (U=0; C=1; A=2; G=3; Rakočević, 1988b) the binary value („weight”) of each codon is obtained, as well as the value of each protein amino acid (as mean values of „weights” of codons taking part in its encoding). The topological system derived in this way based on binary logic and binary numbering system (Rakočević, 1988b), clearly demonstrates that 64 codons can encode exactly 21 different „situations”, i.e. 20 amino acids and a „stop” command (Table 3).

Positions of the eight codons on cube corners actually represent the positions of their mutual „distances” in the topological area of their physico-chemical characteristics. Their positions in the main cube are such that each one of them has its elementary „codon” cube. One has only to imagine the lines linking all the equilibrium points in codon interaction on the faces of the cube. By intersection of these

lines, eight new small cubes — four in the lower row, and four in the upper, are obtained. Using a metaphorical expression, one might say that the „codon” cubes are „empty”, and that the main cube, corresponding to a binary three rosette, is filled with those „empty” small cubes — exactly eight of them. The topological system of the genetic code is further characterized by the fact that one has to imagine (an abstract model) that a third step in the hierarchy is indispensable: the eight main cubes are then „packed up” into a large cube, corresponding to the whole range of eight rosettes on the binary tree, i.e. 64 codons. The correspondence between the cube and the binary tree rosettes is necessary in order to get an information on the relations between the codons, since this is the only way to observe the *optimal* linking of rosettes, at a distance of four bits (as distinguished from three-bit distance between the most different codons in an octade). Only such an optimal four-bit linking of rosettes can be adequately and relevantly translated into a genetic code table (Table 2), which is obviously different from the classical one. By imagining it as a cylinder (but always in terms of a unifying model, i.e. a cube with a sphere inscribed) one can see the direct contact bet-

Table 3. 64 codons for 20 amino acids and 1 "Stop" command.

ween codon groups with U and A as the middle bases and codons with G and C as the middle bases are also in contact. The arrangement of the encoding words (codons) within the genes is in full accordance with this table, (Blalock *et. al.*, 1986; Rakočević, 1988a). Periodicity and complementarity can be read directly from this table; in addition, the pro-

blem of serine and arginine „occupying” two places each, has been solved in this way.

On the basis of the topological genetic code model, it is possible to construct a „mutational amino acid ring” (Fig. 1), which corresponds to the interrelationships between amino acids, first of all in terms of similarity — dissimilarity of their physico-chemical characteristics. In fact, all the relations exactly correspond to the relations between the elements of the cube, as described in introduction.

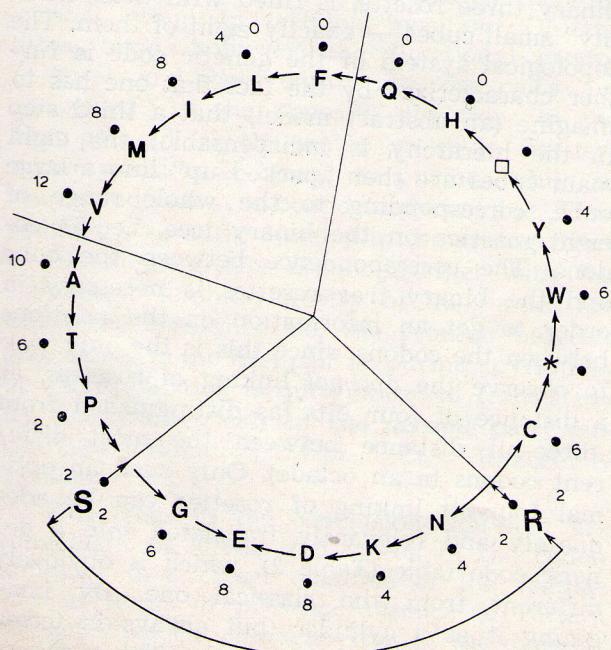


Fig. 1. The optimal amino acid ring

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Rezime

MODELI TRIDIMENZIONAL I KODIT GJENETIK

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Tabela klasike e kodit gjenetik nuk shpreh të gjitha raportet relevante ndërmjet kodonëve. Në këtë punim është treguar se modeli topologjik tridimensional — kubi me tophin e shkruar është burim i të gjitha raporteve të rëndësishme në kodin gjenetik. Nga tetë kodonë të afërt gjeden në majet e kubit edhe atë ashtu që baza e parë është në boshtin x , e dyta në y dhe a treta në boshtin z . Në pajtim me parimin matematikor minimizimi i funksionit binar dhe formës, të tetë kubete të këtilla janë „vendosur” në një kub më të madh (superpozicioni). Ky model është në pajtim të plotë edhe me drurin binar themelor i cili përmban tetë grupe të kodoneve të afërt. Edhe këtu superpozicioni shënon se më parë paketohen degët me nga tetë kodonë të afërt, e mandej edhe kodonët në një degë edhe atë me këtë radhitje: 7 6 4 5 1 0 2 3. Kjo radhitje i përgjigjet rrugës më të shkurtër të lidhjes së majeve të kubit.

Veçoritë fiziko-kimike të kodoneve dhe aminoacideve të tyre gjegjëse janë në pajtim me këtë model topologjik tridimensional. Në model njëkohësisht vërehet edhe ligji i periodicitetit të kodit gjenetik në disa nivele: periodiciteti binar, tetrad, oktad, heksadekad dhe periodiciteti nëpërmjet të numrit 32.

Izvod

TRODIMENZIONALNI MODEL GENETSKOG KODA

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Klasična tablica genetskog koda ne odražava sve bitne odnose među kodonima. U ovom radu pokazano je da je trodimenzionalni topološki model — kocka sa upisanom loptom — izvor svih bitnih odnosa u genetskom kodu. Po osam srodnih kodona nalaze se na temenima kocke i to tako da je prva baza na x

osi, druga na x osi i treća na z osi. Saglasno matematičkom principu minimizacije binarne funkcije i forme, osam ovakvih kocki „smešteno” je u jednu veću kocku (superpozicija!). Ovaj model potpuno je u saglasnosti i sa osnovnim binarnim drvetom koje sadrži osam grupa srodnih kodona. I ovde superpozicija označava da se najpre upakuju grane sa po osam srodnih kodona, a zatim i kodoni na jednoj grani i to sledećim redosledom: 7 6 4 5

1 0 2 3. Ovaj redosled odgovara najkraćem putu povezivanja temena kocke.

Fizičko-hemijske karakteristike kodona i njima korespondentnih amino kiselina u saglasnosti su sa ovim trodimenzionalnim topološkim modelom. Na modelu se istovremeno sagledava i zakon periodičnosti genetskog koda u nekoliko nivoa: binarna periodičnost, tradna, oktalna, heksadekadna i periodičnost preko broja 32.