A.G. MALYGIN

CHART

OF METABOLIC PATHWAYS

(PERIODIC)

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The metabolic pathways chart systemizes the vast up-to-date information on metabolism in periodic form The chart may be of use to specialists in biochemistry, microbiology and related subjects.

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RATIONAL SYSTEMATIZATION OF METABOLIC REACTIONS

Charts of metabolic pathways are a convenient form of recording biochemical information.

Current metabolic charts published by some firms such as ”Koch-Light” (Great Britain, the chart compiled by D.E.Nicholson) [17], ’’Calbiochem” (USA) [16], ’’Boehringer Mannheim” (GFR) [12], are widely known. The structural basis of these charts is made of the best investigated metabolic pathways such as glycolysis, the Krebs cycle, the urea cycle, the pathways of fatty acids metabolism. This structure reflects the process of accumulation of knowledge in the field of metabolism.

The present chart is an attempt at systematization of the vast up-to-date information on metabolism made on the basis of periodic nature of the metabolic pathways network. The very possibility of drawing charts with periodic structure stems from the two principles given below.

The first principle : functionally analogous metabolites usually undergo the same changes forming, as a result, derivatives similar in their chemical functions.

Functionally analogous metabolites are compounds having the identical functional groups (for instance, $-NH_2$,-OH, >CO, -COOH, double carbon-carbon bonds, etc.) as well as certain structural combinations of those groups (for example, combination of a-amino group and carboxyl group in a-amino acids or

double bond and a carboxyl group in the α,β-unsaturated acids, etc.) The following reactions may serve as an example of transformation of a number of functionally analogous compounds into functionally analogous derivatives : reactions of decarboxylation and transamination of α-amino acids which result in the formation of primary amines and α-keto acids respectively and which are typical of all the α-amino acids; reactions of mutual transformation of aldoses, ketoses and polyatomic alcohols; reactions of oxidation and reduction of aldehydes, etc.

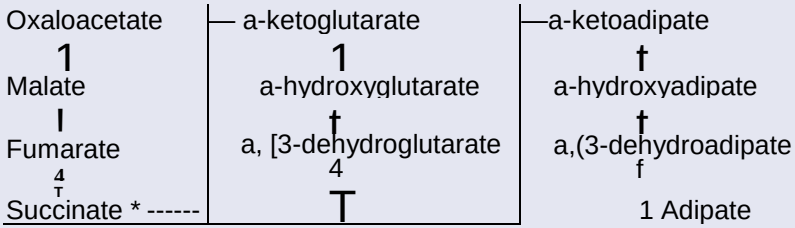
The analysis of the biochemical reactions in view of the principle under consideration allows to group together similar compounds and reactions; moreover, it also allows to distinguish parallel pathways. For example, the sequence of reactions (decarboxylation, deamination, reduction, etc.) is identical for different amino acids. The same is true for monosaccharides, isoprenoids, fatty acids, etc. when metabolic pathways are considered. But this principle works until the compounds take part in reactions involving the centers in which they differ. Thus, the metabolism of aromatic α-amino acids differs considerably from that of heterocyclic α-amino acids in case the reactions involve aromatic nuclei of these compounds.

The second principle: as a result of certain sequences of transformation many metabolites form products which are functional analogs of the initial compounds.

The simplest case is when the analogs are formed as a

result of one reaction, for example, during a step condensation of isopentyl diphosphate or in the case of successive introduction of hydroxygroups into the aromatic ring . More complicated ways of analog formation include several reactions. Thus as a result of several reactions, aspartate forms its analog-glutamate; D-fructose turns into its pentaatomis analog-D-xylulose —as a result of transketolase and transaldolase reactions.

The sequences of reactions meeting the requirements of both principles were found in the network of metabolic pathway during the chart construction. According to the second principle, each of these sequences should lead to the formation of the initial compound analog; then according to the first principle, the obtained analog will undergo tranformations similar to those of the initial compound until a new analog is formed, etc., i.e. the chains of reactions under consideration have a periodic nature. The following sequence of reactions [12, 17] may serve as an example.



Inasmuch as individual metabolites have two or more ways of transformation into their analogs, the chart of ihe metabolic

pathways is a two-dimensional and multi-dimensional network with cells recurring periodically, the cells being complexes of reactions of the same type. The Krebs cyrle may serve as an example of such a two-dimensional cell in the chart; the adjacent cell forms an analogous cycle including compounds which are homologous to ones of Krebs cycle; further on, there are two more similar cells.

Such periodic network may serve as a skeleton around which other reactions of metabolism are grouped and become a natural basis for rational systematization of metabolic reactions.

THE STRUCTURE OF THE CHART

The chart is constructed so as to demonstrate the periodic nature of metabolic pathways network and at the same time to shew the similar structure of certain metabolites. The notion of “a metabolic period” was introduced with that end in view, that is a number of the ways of transformations of a metabolite which are similar to ways of transformations of its analogs which in many cases results in the formation of one of these analogs. As a rule, these periods include, in addition to recurring complexes of some reactions typical of the given period only. Related periods are placed next to each other and form groups The periods arranged in such a way that functionally analogous metabolites aru put in horizontal rows of these periods.

Conventionally the chart may be divided into three parts. The metabolism of the monosaccharides [1, 6, 10] is shown at the top c^{f} the chart. The middle part shows the metabolism of the pyri

dine and purine bases and nucleotides [4, 9, 13, 14, 16], aminoacids [4, 7] and related compounds [1-5, 8, 12, 17]. Located at the bottom part are (from left to right): biogenesis of the primary isoprenoid structures [1, 8, 11, 12, 17], chart of the fatty acid synthesis and degradation [8, 15], and some lipides [4,8, 12,17] as well as biogenesis of main porphyrin structures [1, 12].

The metabolism of the monosaccharides is shown in nine periods. Each period reflects transformations of the monosaccharides with a definite number of carbon atoms. The periods are denoted by arabic figures according to the number of carbon atoms in the structure of the monosaccharides. The periods have much in common but,at the same time,each has its characteristic features. For example, a characteristic feature of the sixth period (6’ subperiod) is a system of metabolic reactions of hexuronic acids the form of which is similar to the system of metabolic reactions of the non-oxidized hexoses. The periods are connected through a system of aldolase and ketolase reactions of the same type. Besides the fifth and the sixth periods are also connected through reactions of decarboxylation of uridine diphosphate derivatives of hexuronic acids.

Horizontally the area of metabolism of monosaccharides is divided into twelve rows. In the first row there are monosaccha- . rides and biphosphates of ketoses; in the second,polyatomic alcohols and their derivatives; in the third,ketoses and their derivatives; in the fourth,aldoses and their derivatives; in the fifth,

aldose - I - monophosphates, in the sixth,uridine diphosphates of aldoses. The row of 2-keto-3-dehydroxyaldonic acids is the symmetry axis of this area inasmuch as the subsequent five rows are similar (as far as the nature of the compounds included therein is concerned) to the five proceeding rows and are a mirror view thereof. Monosaccharides of the subsequent rows have erythro- -configurations of hydroxyls of the third and the fourth carbon atoms while the corresponding hydroxyls of the monosaccharides of the five proceeding rows have threo-configuration.

In order to better organize the chart the chain of glycolysis reactions and some straight ways of transformation of some mono-saccharides into amino acids have a blank space at the point of a-keto acids formation (pyruvate, oxaloacetate, a-ketoglutarate). These ways may be continued as uninterrupted, as the corresponding a-keto acids are found in the middle of the chart.

In the middle of the chart is the metabolism of the amino acids and compounds close to them as far as the metabolism is concerned (different derivatives of the carbonic acids with short carbon chain; aromatic compounds, amines, bases of nucleic acids). The periods of these parts also have similar metabolic pathways. The periods successively connected to each other by analogous reactions, the corresponding compounds of which are differed namber of methylenes $(CH)_2$, may be viewed as homologous. The homologous periods are brought together in the groups. A letter symbol put near a Roman figure shows which

group this period belongs to, the Roman figure showing the ordinal number of the period i.i the group. The letter symbols originate from the words ’’mono-”, ”di-”, ”iso-”, reflecting respectively,the minimum basicity of the acids in groups M and Д and branchen-chain structure of compounds of groups *И* and *W .*

The zero period is in the centc" of the chart and occupies a special position in the system. The compounds i.i the left part of the period(methyl amine, glycine, glyoxylate, formaldehyde, formyate) are homologous to the compounds of the left portion of the first period of group M (ethyl amine, alanine, pyruvate, lactate, acetaldehyde, acetate) while the compounds of its right- -hand part coincide with the compounds of the left-hand part of the first period of group Д (aspartate, oxaloacetate, malate, fumarate, etc.). Thus the zero period may be including into both group and group M. This period comprises some of the reactions of glyoxylate cycle.

Group Д comprises four homologous periods: 1Д period contains the largerpart ofreactions of the tricarboxylic acid cycle and exchange reactions of aspartate.

Considered as the continuation of this period may be the system of reactions of synthesis and degradation of pyrimidine bases containing no methyl group in the fifth position of the pyrimidine nucleus. НД period comprises different reactions related to the metabolism of a-ketoglutarate which comprise the corresponding • reactions of the Krebs cycle, me*abol.c reactions of glutamate as well as the reactions of synthesis and degradation of ornithine, citrulline, arginine (the urea cycle),

proline and their derivatives. 111Д period comprises the metabolic reactions of a-ketoadipate and a-ami noadipate, lysine, homoarginine, homocitrulline and pipecolate. 1\/Д period is represented only by three compounds: a-ketopi melate, a-aminopimelate and adipate.

Located to the left of the zero period is group M, closely o connected with it and comprising two homologous periods. IM period comprises metabolism of pyruvate arid alanine and their derivatives. Connected with this period is a system of metabolic reactions of pyrimidine bases with a methyl in the fifth position of pyrimidine nucleus similar to the corresponding system of reactions connected with 1Д , II M period includes metabolicreactions of a-ketobutyrate and a-aminobutyrate and their derivatives. This period is incomplete inasmuch as it lacks reactions typical of IM period. Group M is characterized by its close connection with biogenesis от sulphur-containing and branched-chain compounds.

Group И comprising metabolic reactions with branched carbon chain includes two homologous periods. 1И period contains metabolic reactions ofvaline and a-ketoisovalerate, НИ period is incomlete; it includes some of the metabolicreactions of leucine and a-ketoisocaproate.

Period И*, which comprises metabolic reactions of isoleucine is not included in group И inasmuch as i.s compounds are net homologous to the corresponding compounds of group И periods. It may be supposed to be the first jperiod of an as yet .unknow group

isomorphic with group И by the structure of its compounds.

Besides the above-described groups consisting of homologous periods in the middle portion of the chart,there are three more groups comprising metabolic reactions of aromatic and heterocyclic amino acids and their derivatives. The corresponding compounds in the periods of these groups differ from each other in the number and position of hydroxyls. The biggest is group A (aromatic) which includes metabolic reactions of phenylalanine, phenylpyruvate and their derivatives [2, 16].It consists of nine periods. The periods are marked by arabic figures which show the position of hydroxyls in the aromatic nucleus. The same group also includes the period containing metabolic reactions of thyroxin inasmuch as it is related to the periods describing the metabolism of phenylalanine and tyrosine.The tryptophan group is marked T (tryptophanic) and consists of two periods:OT period includes metabolic reactions of tryptophan and indole pyruvate; 5T period comprises 5-oxytryptophan and 5-oxyindole pyruvate.

The middle part of the chart ends in the histidine groupand is marked Г (histidine). It consists of one period and includes metabolic reactions of histidine and imidazole pyruvate. The histidine group is closely connected with the above system of reactions of biosynthesis and degradation of purine bases.

Functionally analogous compounds of the periods of the chart middle portion are arranged in rows. The names of rows common to all the periods are given on the left thereof. These

are rows of amines and their methyl derivatives, a-amino acids, a-keto acids, a-hydroxy acids, a,p-unsaturated acids, (3-hydroxy acids, p-keto acids, primary alcohols [3], aldehydes and saturated carboxylic acids. The names of the rows belonging to group Д only (cyclic saturated and unsaturated amino-acids, guanido- and ureidc a-amino acids, diamines, betaines, etc.) are located to the right.

Arranged between the rows of a-amino acids and a-keto acids is a row of triplets of the genetic code depicting the inclusion of the corresponding amino acids into proteins. Some triplets are not found in this row because the amino acids coded by them are placed at the other parts of the chart. Inasmuch as a-ami noadipate occurs in the proteins of some plants [7], the possibility of the existance of a number of triplets coding it is postulated by the ”?“ sign.

The diagram of the biogenesis of the basic isoprenoids structures is located in the left-hand bottom corner of the chart.

The initial compounds for the biogenesis of these structures are,on the one hand,acetoacetate, and on the other, 3-methyl- glutaconate which is formed as a result of 3-methyl-crotonate carboxylation in the presence of biotin. Acetoacetate and 3-methyl- glutaconate are interconnected through a system of reactions resembling in their nature the reactions in 1Д, IM and IИ periods. The final product of these reactions is mevalonate, which is the immediate precursor of isopentenyl and dimethylallyl-diphosphate

active Cg-units of biosynthesis of isoprenoid structures.Stepwise condensation of Cg-units results in the formation of isoprenoid compounds in the form of chains with 5, 10, 15 and 20 carbon atoms; in the chart they are in the horizontal row.The certain groups of terpenoid compounds stem from each of the above compounds. Transformations of the compounds of these groups may be considered as periods inasmuch as the structures 'of their compounds are homologous. The homologous difference is a Cg- or double Cg-unit depending on the row. One of the periods, for example, is a Cig-(C-|5)2 period,which includes the metabolism of steroids.

A short diagram of the anabolism and catabolism of fatty acids is in the bottom of the chart. It is indicated through B and shows the succession of reactions of ^-reduction and p-oxidation of fatty acids with malonyl-CoA and acetyl-CoA, respectively. Inasmuch as the data on similar reactions of methylmalonyl-CoA and propionyl-CoA are known in the literature, the chart also contains a similar diagram of the synthesis and degradation of branched- -chain fatty acids marked through p'. A chart of metabolic reactions of some lipids is placed below.

The metabolism of porphyrin compounds is in the right-hand bottom part of the chart. The initial compound for the biosynthesis of porphyrins is 5-ami no levulinate obtained from glycine and succinyl-CoA. As a result of condensation, two molecules 01 5-aminolevulinate form one molecule of porphobilinogen which is

used in the synthesis of porphyrins I, porphyrins III and corrinoids.

In the chart the reactions are marked with arrows. The corresponding enzymes are denoted near the anows by digital code according to the International Enzyme Nomenclature [9, 13]. The corresponding references may be found in the Reference Guide of Enzyme Nomenclature with the help of this code.

Tne artQws of corresponding colour mark the reactions in which pyridoxal phosphate, thiamine pyrophosphate, lipoate, NAD or NADP and riboflavin derivatives take part. In other cases abbreviated names of coenzymes are put above the arrows.

If a compound takes part in several analogous reactions it is usually presented in the chart in the abbreviated form.e.g. in the reactions of aldol condensation dihydroxyacetone-phosphate has an abbreviated form ДОАФ. In some cases,when the nature of the compound taking part in the reaction is obvious (for example, ammonia in the reactions of transamination or oxidizing deamination) this compound is not given in the chart.

To save room and preserve the symmetry instead ofthe full formula of some trivial derivatives,only the chemical groups which distinguish them from the initial compounds are given in the chart. These groups are put into brackets which are placed near the substituted atoms (or groups) of the initial compounds. Code figures of the enzymes catalyzing the reactions which connect the basic and derived compounds are put near the brackets, Reactions related to such derived compounds are denoted by arrows broken at

the corresponding ends (refer to the legend in the chart).

In order to divide the periods and rows more distinctly colour areas are used.

POSSIBLE FIELDS OF APPLICATION OF METABOLIC CHARTS

The advantages offered by the metabolic charts as compared with other ways of recording biochemical information consist in the possibility to give the main data on metabolic pathways using up minimum space. This information given in the form of a branched net of biochemical reactions allows to follow the ways of transformation of different substances in the process of metabolism and judge upon their role in this process.

These charts may help to predict changes in metabolism due to the inhibition of certain biochemical reactions as well as to detect the influence of the repression and induction of certain enzymes on metabolism. Therefore, the charts may be of sub - stantial aid in the analysis of the ways of metabolic regulation.

Schematic diagram of metabolism of substances is universal for all animate nature. However, at the same time there are essential differences in the metabolism of the organisms of different. types. These differences can be shown in the metabolic charts. The laws of biochemical evo.ution may be revealed on comparing metabolic charts of organisms of different types. These charts are

also used in the study of mutagenesis after-effects, for example, to predict the influence of certain mutations on metabolism. This may find application in the analysis of molecular mechanisms of various hereditary diseases and in research of possible ways of struggle with them. These charts may also be used in planning the works on gene engineering. Inasmuch as metabolic charts comprise vast data on metabolism and show visually the whole metabolic diagram they may serve as a useful reference guide in biochemistry.

The present chart offers some additional possibilities. The periodic construction of the chart supposes recurrence of the structures of its definite parts which makes it possible to predict with certain probability the existence of yet unknown compounds and reactions. Blank colour areas in some cases indicate the possibility of the existence of compounds functionally analogous to the corresponding compounds in the neighbouring. The incomplete periods of amino acids metabolism as well as the fourth, seventh, eighth and ninth periods of monosaccharides metabolism may be perspective for the search of new compounds and reactions.

The present chart may be possibly used for better systematization of enzymes.

As it is in the present chart, the metabolism diagram may also be of use in considering certain aspects of the evolution of the enzyme system of a cell and thus the evolution of genome. In this

respect it is, for instance, interesting that the middle nucleotides of codons are similar for all amino acids contained in the homologous periods of a given group. The latter may point to the fact that the evolution of the structure of codons to a certain extent is determined by the common character of metabolism of amino acids coded by them.

We hope that the present chart may be useful in studying and teaching biochemistry inasmuch as it facilitates the study of metabolic processes allowing to see it as a united and regular system of reactions. The periodicity of the chart allows to study a wide range of problems common to all periods of similar type on the example of one of the periods and facilitates memorizing of large amout of information.

The detailed description of biochemical processes is not the subject of the present chart; therefore, many metabolic pathways are shown schematically. For fuller information on any section of metabolic pathways turn to the references the list of which is given below.

The present variant of the chart is not final. The chart may be changed and amended as new experimental data will be accumulated and more careful analysis of the up-to-date material will be made. Therefore, the author will be thankful for any critical remarks.

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TRANSLATION OF CHART TEXT

PERIODIC CHART OF METABOLIC PATHWAYS

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The system of metabolic pathways is presented as a chart in the form of a network of reaction with periodically recurring complexes of reactions (periods). This became possible inasmuch as many functionally analogous metabolites undergo similar succession of transformations which result in the formation of structural analogs of the initial compounds.

Presented at the top part of the chart is a diagram of monosaccharide metabolism. It comprises twe've horizontal rows (their names are to the left of the rows) and nine vertical periods denoted by arabic numerals in accordance with the number of carbon atoms in the monosaccharides of the given period.

The diagram showing metabolism of amino acids and related compounds is at the central part of the chart. Rows of products of decarboxylation, deamination, oxidation, otc. are placed above and below the row of a-amino acids. Vertical periods are united in several groups on the principle of common nature of metabolism. These groups arj denoted by letters. Periods in the groups of aliphatic compounds are denoted by Roman numerals. Periods in the groups of aromatic and heterocyclic compounds are denoted by arabic figures (accoiding to

the position of hydroxyl groups in the nucleus).

Presented at the bottom part of the chart is the diagram of isoprenoid compounds biogenesis, metabolic diagrams of non-branched-chain (P) and branched-chain (p') fatty acids, some lipids and the diagram of porphyrin compounds biogene sis.

LEGEND

Numerical codeisgiven for enzymes included in the nonfenclature ’’Enzyme Nomenclature” , ’’VINITI” Publishing House, Moscow, 1966; ’’Enzyme Nomenclature”, New York, 1972. The position of the figures at the horizontal, sloping and vertical arrows is shown.

lX]-in ROH[X| or RHlX] indicates the existence of RX derivative formed when the corresponding H or OH is replaced by X. When the names of the derivatives in that case are given they are * /x/ᶻ taken into brackets, я он зли t.7. LI r The arrows denoting the initial compounds ROH, RH are continuous. Arrows denoting derivatives RX are broken at the corresponding ends. The nomenclature codes of enzymes catalyzing the formation of derivatives from the initial compounds and enzymes hydrolyzing derivatives into initial compounds are placed near [X].

Heavy arrows linking the rows denote reactions common to the given rows of compounds and being catalyzed by one enzyme or a group of related ones.

(j Other names of the corresponding compounds are placed in parentheses.

Coenzymes.

Rectangulars near the corresponding amino acids contain codones of genetic code.

? Areas requiring clarification.

In bold type are the structural formulae and the names of the compounds participating in the reactions of the main metabolic cycles.

REACTIONS WITH PARTICIPATION (OR ALLEGED PARTICIPATION) OF COENZYMES

-------- ►Blue continuous arrow-pyridoxal phosphate

■■ » Red continuous arrow-thiamine pyrophosphate

-------- ► Red thin continuous arrow-.ipoate

-------- * Green continuous arrow-FMN or FAD

-------- Violet continuous arrow-NAD or NADP'

Black continuous arrows:

———► cobalamin

At*HoA г acetyl coenzyme A

ь biotin

Tra> г tetrahydrofolate

....f for all other reactions

» ,1- „ several reactions succeeding each other

—► —* inde nite number of reactions

> Formulaes are given in the chart

ABBREVIATIONS IN THE CHART

ЛИ -Acetyl

АНКАР -5'-phosphoribosyl-5-amine 4-im'dazole-carboxamid

АПБ - Acyl -carrier-protein

г* - Glycolaldehyde bonded with transketolase

дом - Di hydroxyacetone phosphate

- Di hydroxyacetone bonded with transketolase *nlt* - Coenzyme A * - Urea

оиоц - Oxalacetate л»? . Pyruvate

- Phosphoeno I pyruvate

р - Ribosyl *ф* - Phosphate - Diphosphate ф/> -5-phosphoribosyl *ФРФФ* -5-phosphori bosy l-l-d iphosphate *фд* - Phosphatidyl

4 - Deoxy- (in the nomenclature of nucleotides and nucleosides)

x - Adenosine

г - Guanosine

п - Inosine

к - Xanthosine

ц - Cytidine

y - Uridine

г - Thymidine

нмф - Nncleoside-5'-monophosphate 1 H - the corres- *ндф* - Nucleoside-5'-diphosphate ponding ribo - *итФ* - Nuclooside-5'-triphosphate J or deoxyribonucleoside

НАД ~ Nicotinamideadeninedinucleotide *НАДФ* - Nicotinamideadeninedinucleotide phosphate *ФМН* - Flavinemononucleotide *ФАД* - Flavineadeninedinucleotide *Я* - Organic radical

* Fatty acids with a long carbon chain are formed or degradated at Acyl-CoA repeated passage along the path of the P (P') reduction or, correspondingly, p (P') oxidation.

You may obtain "Chart of Metabolic Pathways,(periodic)"/ in Russian) by A.G.Malygin with the discription in English enclosed by writing directly to the Shemyakin Institute of Bioorganic Chemistry at the address listed below:

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