Enzymatic Synthesis of a Blood Group B-related Pentaglycosylceramide by an α-Galactosyltransferase from Rabbit Bone Marrow*

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MANJU BASU† AND SUBHASH BASU
From the Department of Chemistry, Biochemistry and Biophysics Program, University of Notre Dame, Notre Dame, Indiana 46556

SUMMARY

An α-galactosyltransferase that catalyzes the biosynthesis in vitro of blood group B-specific pentaglycosylceramide from UDP-[14C]galactose and α-O-β-galactosyl (1→3)-O-β-(N-acetyl) glucosaminosyl (1→3)-O-β-galactosyl (1→4)-O-β-glucosyl (1→1) ceramide was detected in homogenates of adult rabbit bone marrow. The enzyme was present in the supernatant solution obtained after homogenization of rabbit bone marrow in the presence of 0.6% Triton X-100 and centrifugation at 100,000 × g. The enzyme was precipitated from the supernatant solution at 0 to 45% saturation with ammonium sulfate. The 14C product of the reaction was isolated, purified, and analyzed for its constituents. It inhibited the hemagglutination reaction of human B-type cells and rabbit erythrocytes against human anti-B serum. The terminal [14C]galactose was cleaved 85% by the action of α-galactosidase. The Km values were 1.67 × 10⁻³ M and 1.43 × 10⁻⁴ M for the tetraglycosylceramide (LacTet-cer) and UDP-galactose, respectively.

The chemical structure of blood group-specific glycoproteins isolated from cyst fluid and stomach mucosal linings has been elucidated by Morgan (2), Watkins (3), and Kabat (4). On the other hand, the blood group-specific substances isolated from erythrocyte membranes appeared to be glycosphingolipids, and the structures of those isoantigens were described by Yamakawa (5), Hakomori (6), and Kocicak et al. (7). The specificity of blood group substances is determined by the specific oligosaccharide chains attached to the glycoprotein or ceramide moiety. Elov et al. (8) have reported the complete chemical structure of a blood group B-specific pentaglycosylceramide (α-O-galactosyl (1→3)-O-β-galactosyl (1→3)-O-β-(N-acetyl) glucosaminosyl (1→3)-O-β-galactosyl (1→4)-glucosyl (1→1)ceramide) which they isolated from rabbit erythrocytes. The structures of the Leα- and Leβ-specific glycosphingolipids isolated from human adenocarcinoma tissues were described by Hakomori et al. (9, 10). We have reported previously (11, 12) the biosynthesis in vitro of the core tetraglycosylceramide (Gal1→3GlcNAc 1→3Gal1→4Glc 1→1 ceramide) from a triglycosylceramide containing N-acetylgalactosamine. The present studies are concerned with the transfer of galactose to the tetraglycosylceramide to form a blood group-specific pentaglycosylceramide. The reaction, catalyzed by an α-galactosyltransferase also obtained from rabbit bone marrow, is as follows.

\[
\text{UDP-[14C]galactose} + \text{Gal} \rightarrow \text{UDP} - \text{N-acetyl-}[\text{14C}]\text{galactosamine} + \text{UDP} - \text{galactose, respectively.}
\]

EXPERIMENTAL PROCEDURE

Materials

The following materials were obtained from commercial sources: Whatman No. 3MM paper (W. and R. Balson, Ltd., Maidstone, Kent, England); Adsorosil-I (Applied Science Laboratories, State College, Pennsylvania); Unisil (Clarkson Chemical Company, Williamstown, Pennsylvania); UDP-[14C]galactose, UDP-N-acetyl-[14C]galactosamine, UDP-[14C]glucose, and UDP-N-acetyl-[14C]glucosamine (New England Nuclear Corporation); hexokinase, galactose dehydrogenase, and glucose-6-P dehydrogenase (Sigma); erythrocytes and bone marrow of mature rabbit (Pel-Freez Biologicals, Rogers, Arkansas); human anti-A, and anti-B blood grouping serum (Hyland Division Travenol Laboratories, Inc., Costa Mesa, California, and Lederle Laboratories Div.). Glycosphingolipid acceptor was isolated from erythrocytes by our previously published method (12). Other substances were either commercial preparations or gifts.

Methods

Analytical Procedures—Protein was determined by the method of Lowry et al. (13). The [14C] product of the enzymatic reaction and the acceptor glycosphingolipid were methanolized by the procedure of Kishimoto and Radin (14). Sphingosine was determined by the spectrophotometric method of Lauter and Trans...
into a coiled glass column (4 feet acetone or chloroform; 0.5 to 1.0 ml of the solution was injected. The residue was dissolved in 50 to 100 ml of analytical grade form layer (chloroform-water, 2:1, v/v) and dried under nitrogen. 

was added to the residue, which was heated at 120°C for 3 hours; the layer was evaporated to dryness under nitrogen six times with 5

volumes of ethyl acetate and the pH of the lower, aqueous layer was dried under 

nitrogen. The residue was dissolved in 2.0 ml of 1 N HCl for 1 hour at 100°C. The hydrolysate was extracted with 5 volumes of ether and the lower, aqueous layer was dried under nitrogen. The residue was dissolved in 0.1 ml of 1 N HCl and 5 volumes of sucrose-EDTA-mercaptoethanol containing Triton X-100 (6 mg per ml) and then was centrifuged for 2 hours at 100,000 x g. The enzyme activity was precipitated by 0 to 45% saturation with ammonium sulfate from the clear, reddish supernatant and collected by centrifugation at 100,000 x g for 30 min. The pellet was then dissolved in 1 to 2 volumes of sucrose-EDTA-mercaptoethanol-Triton X-100 and was used as the enzyme source, designated fraction 45R. All studies reported here were conducted with this fraction. Further purification of the α-galactosyltransferase activity is currently under investigation.

Enzyme Assays—Complete incubation mixtures contained the following components (in micromoles unless otherwise stated) in final volumes of 0.025 ml: LacTet-ceramide, 0.10; Triton CF-54, 240 µg; caddylate-HCl buffer, pH 7.29, 5.0; MnCl₂, 0.25; UDP-[³⁵C]galactose, 0.044 (2.2 x 10⁶ cpm per µmole); enzyme, fraction 45R (contained 30 µg of Triton X-100), 0.10 mg of protein. After 1 hour at 37°C, the mixtures were assayed by high voltage electrophoresis followed by chromatography, as described in the text. Under these conditions, the rate of reaction remained constant with time of incubation up to 1 hour, and was proportional to protein concentration up to 0.10 mg/0.025 ml of incubation volume.

| Incubation mixture | [³⁵C]Pentaglycosylceramide nmoles/mg protein/hr |
|--------------------|-----------------------------------------------|
| Complete           | 14.15                                         |
| Minus LacTet-ceramide | 0.17                                          |
| Minus MnCl₂        | 0.18                                          |
| Plus EDTA (2.5 µmoles) | 1.18                                         |
| Minus Mn²⁺, plus Co²⁺ or Cd²⁺, Zn²⁺, Ni²⁺ | 1.85-3.91                                   |
| Minus active, plus heat-inactivated enzyme (3 min, 100°C) | 0.07                                       |

Preparation of Enzyme—The α-galactosyltransferase was detected in homogenates of rabbit bone marrow. All steps in the preparation of enzyme were conducted between 0° and 5°. Rabbit bone marrow (20 to 25 g, purchased frozen) was homogenized with 3 volumes of 0.32 M sucrose containing 0.001 M EDTA and 0.014 M mercaptoethanol, at pH 7.6, in a Potter-Elvehjem homogenizer with a loosely fitting Teflon pestle. The homogenate was filtered through a double layer of cheesecloth to remove fat and then was centrifuged in a Spinco L2-65S centrifuge for 90 min at 100,000 x g. The pellet was resuspended with 2 volumes of sucrose-EDTA-mercaptoethanol containing Triton X-100 (6 mg per ml) and then was centrifuged for 2 hours at 100,000 x g. The enzyme activity was precipitated by 0 to 45% 

1 J.-L. Chien and S. Basu, unpublished experiments.
Incubation mixtures contained the same components as in Table I, except that varied concentrations of tetraglycosylceramide were used. After 1 hour at 37°C, the incubation mixtures were assayed by high voltage paper electrophoresis as described in the text. The inset shows a Lineweaver-Burk plot of the same data.

Substrate Competition—We previously reported the presence of a β-galactosyltransferase activity in rabbit bone marrow (12) that catalyzes the transfer of galactose from UDP-galactose to the triglycosylceramide (GlcNac → Gal → Glc → ceramide) to form tetraglycosylceramide. It remains to be determined whether the α-galactosyltransferase activity which catalyzes the transfer of galactose from UDP-galactose to the tetraglycosylceramide (Gal → GlcNac → Gal → Glc → ceramide) is the result of a single transferase with dual specificities or is due to the presence of two different galactosyltransferases. To obtain definite information on this question, competition experiments were conducted as shown in Table III. Incorporation of galactose was determined in the presence of LacTri-ceramide and LacTet-ceramide first separately and then together. The quantity of galactose (27.44 nmoles) incorporated into the mixture was close to the theoretical value (26.93 nmoles) expected if two enzymes were involved in each case. A value of 15.72 nmoles was calculated for single enzyme catalysis with both substrates, using Equation 1. Further information on the presence of two different galactosyltransferases (α and β) in fraction 45R was obtained from the following studies on galactosidases.

Isolation, Characterization, and Analysis of [14C] Product—The [14C]product was isolated from a large scale (20-fold) incubation mixture. The radioactive product was treated with 0.6 N NaOH and remained constant with time of incubation up to 1 hour. A pH optimum of 7.29 was exhibited in cacodylate-HCl buffer.

Donor Specificity—The requirement for UDP-galactose as galactose donor could not be substituted by any of the following sugar nucleotides: UDP-glucose, UDP-N-acetylglucosamine, or UDP-N-acetylgalactosamine (<3%). The rate of the reaction was changed no more than 5% by the addition of non-radioactive galactose, which indicated that free galactose was not incorporated into the pentaglycosylceramide. The effect of varying the concentration of UDP-[14C]galactose on the rate of the reaction is shown in Fig. 1. The calculated K_m value for UDP-[14C]galactose is 0.14 mM.

Effect of Substrate Concentration and Substrate Specificities—The effect of varying the concentration of tetraglycosylceramide (LacTet-cer) on the rate of the reaction is shown in Fig. 2. The calculated K_m value is 1.67 mM. The results of studies with different potential lipid acceptors are shown in Table II. Asialoganglioside, Ta-y-Sachs ganglioside (GM2), lactosylceramide, and ceramide (containing 2-hydroxystearic acid) were completely inactive under these assay conditions. Lac-nTet-ceramide was almost as active as LacTet-ceramide. The significance of the high activity of the LacTri-ceramide is discussed in the following section. The acceptor specificity of the α-galactosyltransferase was tested with a number of different oligosaccharides. Lacto-N-tetraose, and N-acetyllactosamine were the most active acceptors. 2′-Fucosyllactose and lacto-N-fucopentaoses I and II were poor acceptors. The significance of these results is considered under "Discussion."
### Table II

**Substrate specificity studies with enzyme fraction 45R obtained from rabbit bone marrow**

Conditions were the same as described in Table I, except that different potential acceptors were added as indicated below. After 1 hour at 37°, the incubation mixtures were assayed by high voltage paper electrophoresis as indicated in the text.

| Potential acceptor                      | Structure | Concentration | U[14C]Galactose incorporated |
|----------------------------------------|-----------|---------------|-----------------------------|
| Endogenous                             |           |               | 1.27                        |
| Lactose                                | Gal 1→4 Glc | 6.4           | 7.13                        |
| Lactosamine                            | Gal 1→4 GlcNAc | 5.6           | 18.70                       |
| 2'-Fucosyllactose                      | Gal 1→4 Glc | 3.5           | 1.56                        |
| Lacto-N-tetraose                       | Gal 1→3 GlcNAc 1→3 Gal 1→4 Glc | 5.2 | 16.77                     |
| Lacto-N-fucopentaose I                 | Gal 1→3 GlcNAc 1→3 Gal 1→4 Glc | 6.0 | 4.12                      |
| Lacto-N-fucopentaose II                | Gal 1→3 GlcNAc 1→3 Gal 1→4 Glc | 6.0 | 3.63                      |
| LacTet-cer                             | Gal 1→3 GlcNAc 1→3 Gal 1→4 Glc | 4.0 | 14.15                     |
| Lac-nTet-cer                           | Gal 1→4 GlcNAc 1→3 Gal 1→4 Glc 1→1 ceramide | 4.0 | 12.89                     |
| Asialoganglioside                      | Gal 1→3 GalNAc 1→4 Gal 1→4 Glc 1→1 ceramide | 4.0 | 1.97                      |
| Tay-Sachs ganglioside (GM3)            | GalNAc 1→4 Gal 1→4 Glc 1→1 ceramide | 4.0 | 1.94                      |
| LacTri-cer                             | GlcNAc 1→3 Gal 1→4 Glc 1→1 ceramide | 4.0 | 32.50                     |
| Lactosylceramide                       | Gal 1→4 Glc 1→1 ceramide | 4.0 | 2.21                      |
| Glucosylceramide                       |   | 4.0           | 2.70                        |
| Ceramide                               | 2-Hydroxystearic acid-Sphingosine | 4.0 | 1.15                      |

in methanol for 1 hour and then dialyzed overnight against distilled water. The radioactive product (0.06 µmole) remaining inside the dialysis bag was further purified by Unisil column chromatography (recovery, 87%), and eluted with chloroform-methanol (60:40, v/v) and by thin layer chromatography (Adsorbosil-1; recovery, 55%). The [14C] product co-chromatographed with nonradioactive pentaglycosylceramide isolated from rabbit erythrocytes (Fig. 3). The [14C] product was analyzed directly for [14C] and for its constituents after methanolysis, followed by acid hydrolysis. The molar ratios of its constituents were: sphingosine, 1.00 (methyl orange (15)); glucose, 0.98 (hexokinase, glucose-6-P dehydrogenase (16)); galactose, 2.83 (galactose dehydrogenase (17)); hexosamine, 0.98 (modified Morgan-Elson reaction (18)); and [14C], 0.83 (based on the specific activity of the UDP-[14C]galactose). The only [14C]-sugar detectable after hydrolysis was [14C]galactose (identified by paper
TABLE III

Substrate competition experiments

Conditions were the same as described in Table I, except that the indicated substrates or substrate mixtures and a different batch of enzyme fraction 45R were used. After 1 hour at 37°C, the incubation mixtures were assayed by high voltage paper electrophoresis as described in the text.

| Substrates | Concentration | Theoretical for | β product |
|------------|---------------|-----------------|-----------|
|            |               | One enzyme | Two enzymes |
| GlcNAc → Gal | 1 3 1 4 1 1 | 2.0 | 16.86 |
|            | β |              |           |
| Gal → GlcNAc → Gal | 1 3 1 4 | 8.0 | 10.07 |
|            | β |              |           |
| Glc → cer (LacTri-cer) | 1 1 | 2.0 + 8.0 | 27.44 15.72 26.93 |

The following equation was used to calculate the value for the one-enzyme theory:

\[
v_t = \frac{V_a(a/K_a) + V_b(b/K_b)}{1 + (a/K_a) + (b/K_b)}
\]

where \(a \) and \(b \) are the concentrations of LacTri-cer and LacTet-cer, respectively; \(K_a \) and \(K_b \) values for two substrates are, \(K_a = 5.0 \times 10^{-4} \) M and \(K_b = 16 \times 10^{-4} \) M; and \(V_{max}, V_a \), and \(V_b \) are 21.26 and 14.5 nmoles per mg of protein, respectively.

Calculated value for the two enzyme theory, \(v_t = v_a + v_b \)

chromatography, borate electrophoresis, and as an active substrate of galactose (dehydrogenase).

Inhibition of Hemagglutination Reaction—The blood group B specificity of the 14C product was measured by the standard hemagglutination inhibition technique of Hakomori and Strycharz (10). The glycosphingolipid to be tested was dissolved in chloroform-methanol (1:1) and was transferred (1 to 15 μg) to micro-test tubes (7 × 75 mm). The solvents were evaporated under nitrogen and the glycosphingolipid was dissolved in 10 to 15 μl of 0.85% NaCl. The mixtures were heated for 10 to 15 min at 60°C and cooled to room temperature before addition of antiserum and cells. In the absence of any glycosphingolipid the positive hemagglutination reaction was tested upon addition of 10 μl of 6% cell suspension (human B-type erythrocytes or rabbit erythrocytes) to 5 μl of anti-B human serum (purchased from Hyland Laboratories, Costa Mesa, Calif.). Inhibition of the hemagglutination reaction was not observed with human B-type red cells until the concentration of nonradioactive pentaglycosylceramide (or 14C product) reached 3 μg/0.025 ml level (Table V). The hemagglutination inhibition reaction was also observed with rabbit erythrocytes in the presence of nonradioactive pentaglycosylceramide (minimum concentration 5 μg/0.025 ml) and 14C product (6 μg/0.025 ml).

Fig. 3. Radioautogram of 14C product. 1, Gal-Gal-Glc-ceramide; 2, Gal-GlcNAc-Gal-Glc-ceramide; 3, GalNAc-Gal-Gal-Glc-ceramide; 4, Gal-Gal-GlcNAc-Gal-Glc-ceramide; 5, 14C product (before chromatography on Unisil, 10,000 cpm, x-ray plate exposed for 7 days). Solvent was chloroform-methanol-water (60:35:5, v/v/v); Silica Gel G.
TABLE V
Inhibition of hemagglutination reaction by pentaglycosylceramides

The technique of hemagglutination inhibition reaction has been described in the text; + indicates presence of agglutination and - indicates absence of agglutination. A and B represent two separate experiments performed under identical conditions except for the indicated glycolipids.

| Glycolipid added | Incubation |
|------------------|------------|
|                  | (A) Pentaglycosylceramide (B) Hex product | Hemagglutination reaction |
| Anti-B serum to human D-type red cells | µg/0.025 ml | + |
| 0                | 0          | + |
| 1                | 1          | + |
| 2                | 2          | + |
| 3                | 3          | - |
| 6                | 6          | - |
| 9                | 9          | - |
| Anti-B serum to rabbit red cells | 0, 2.5, 5, 10, 20 | + |

DISCUSSION
The structure of the blood group B-specific pentaglycosylceramide isolated from rabbit erythrocytes has been shown to contain terminal galactose linked (α1 → 3) to the penultimate β-galactopyranosyl residue (8). The present study was performed to demonstrate the activity of an α-galactosyltransferase in mature rabbit bone marrow that catalyzes the incorporation of galactose into tetraglycosylceramide to form the blood group B-specific pentaglycosylceramide. The above experiments demonstrate that enzyme fraction 45R obtained from mature rabbit bone marrow contains at least three different galactosyltransferases, lactose synthetase (24-26), UDP-galactose:LacTri-cer α-galactosyltransferase, and the UDP-galactose:LacTet-cer α-galactosyltransferase. In previous communications (11, 12) we presented evidence which suggested that the first two reactions are catalyzed by two different β-galactosyltransferases. Substrate competition experiments (Table III) suggest strongly that the α-galactosyltransferase activity is different from that of the other two β-galactosyltransferases. On the basis of substrate specificity studies (Table II) and the substrate competition studies, the α-galactosyltransferase was distinguished from three other β-galactosyltransferases previously obtained from rat and embryonic chicken brains that catalyzed steps in the synthesis of cerebrosides (27-29) and gangliosides (30-33). Treatment of [14C]pentaglycosylceramide with testicular galactosidase released 85% of [14C]galactose, whereas only 2% of [14C]galactose was released by the action of testicular β-galactosidase.4 Testicular galactosidase cleaves both the α1 → 3 and α1 → 4 linkages (33). It is possible that the [14C]pentaglycosylceramide synthesized by the α-galactosyltransferase described in this paper might be either O-α-galactosyl (1 → 3)-LacTet-ceramide, O-α-galactosyl (1 → 4)-LacTet-ceramide, or a mixture of both. It also appears from the substrate specificity studies (Table II) that both LacTet-ceramide and Lac-nTet-ceramide are almost equally active as acceptors. Further studies of the structure of the enzymatic product are in progress.

Recently Hearn et al. (34) have reported the isolation of a UDP-galactose:glycoprotein α-galactosyltransferase from ovarian cyst fluid which transfers galactose only to oligosaccharides in which L-fucose is attached to the terminal β-galactose by an α-1 → 2 linkage. The present studies show (Table II) that the most active acceptors are those containing a β-galactopyranosyl residue at the nonreducing end without fucose attached to it, such as N-acetyllactosamine, lacto-N-tetraose, lactose, and...
Each reaction is catalyzed by a specific glycosyltransferase and requires the corresponding sugar nucleotide. A β-N-acetylglucosaminyltransferase that catalyzes Reaction 1 to form the triglycosylceramide (LacTri-cer) is also present in rabbit bone marrow (36).\(^\dagger\) It seems likely that the lactosylceramide is an intermediate in the biosynthesis de novo of blood group-specific glycosphingolipids or gangliosides (37-39) or is a precursor of globosides (37) and Forssman hapten (38, 39).

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